Factors influencing the distribution and spread of an invasive weedy species, *Erythranthe guttata*.

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Abstract

Erythranthe guttata is a riparian weed common to Europe and Australasia and is widespread in its native USA. The plant readily colonises damp areas such as stream banks, waterways, hillside seeps and road gutters. It forms a dense mat of stoloniferous growth that rapidly crowds out neighbouring plants. *E. guttata* propagates easily through clonal tissue fragments during mechanical clearance or flood events. Understanding the factors influencing the distribution and performance of *E. guttata* is of value for managing its spread. In this thesis my focus was on a fine scale assessment of the factors limiting distribution and spread of *E. guttata.* To achieve this, I carried out two field surveys to assess the influence of key biotic and abiotic factors on the occurrence and abundance of *E. guttata* on Banks Peninsula, New Zealand. I based the choice of factors on a Scottish study by Truscott, et al. (2008a). In addition to the field surveys and based on their findings, I carried out four greenhouse experiments to test for i) the influence of shading and interspecific competition and their interaction, on *E. guttata* performance measures and ii) whether *E. guttata* populations in the region show evidence of a persistent soil seed bank.

Both field surveys showed that several biotic and abiotic factors, including shading, local biota and habitat type, are significantly associated with *E. guttata* presence and abundance. Critically, the findings of the surveys showed that while some factors such as shading intensity affected distribution similarly in Scotland and New Zealand, others had no effect in New Zealand; substrate type and availability of sediment patches. Knowing this is of value tin the prediction of the potential spread of *E. guttata* across Banks Peninsula and more widely in New Zealand and provides a unique New Zealand context to the ecology of this widespread weed.

The greenhouse experiments into shade and competition effects showed that while shade has a strong negative influence on *E. guttata* performance, contrary to my expectations, no evidence was found for a significant interactive relationship between shading intensity and interspecific competition. The greenhouse experiments investigating soil seed banks found evidence for a persistent, overwintering *E. guttata* seed bank in Banks Peninsula populations.

The results of my study show that some of the same factors influencing *E. guttata* distribution in Scotland may be of value in predicting its spread in New Zealand, however further work is needed to understand all key factors important in New Zealand. Overall, the results of my study have improved our understanding of the ecology of this invasive weed in New Zealand and in addition will underpin future studies into the reproductive ecology and invasion biology of *E. guttata* across New Zealand.

Chapter 1

1. Introduction

1.1 Invasion Biology

The study of biological invasions primarily concerns the performance of species transported to novel environments. Due to the vast increase in global trade since the beginning of the 20th Century, transportation of alien species has massively increased in volume and frequency (Levine and D'Antonio, 2003). Exotic invasive species establishment and success is also predicted to increase due to the effects of climate change (Bradley, et al., 2011; Seebens, et al., 2015) Invasions have far-reaching and profound effects on the ecology and biodiversity of invaded areas, disrupting native ecosystems (Parr, et al., 2012) and causing damage to agriculture, national economy and human health. (Sakai, et al.;2001, Drake, 1989; Anadon, et al., 2014; Perrings, 2001). Early detection of invasions and development of control methods is critical to preventing potentially irreversable damage to the ecological and economic interests of a nation.

1.1.1 Definition and stages of invasion

All invasions begin with an introduced population, however, not all introductions result in a species becoming invasive. The term is often misused to describe all species that are introduced into a novel region, particularly if they are notably undesirable. Individuals may successfully reproduce within the novel environment but fail to establish as their long-term population

growth is negative. A successful invasion may involve several or even hundreds of semi-concurrent waves of introduction, survival and reproduction for an introduced species to progress to a viable population size (Richardson, et al., 2000). Therefore, the term ‘invasion’ refers to introduced populations that sustain rapid expansion in size, while establishing new populations further afield in the host environment (Mack, et al., 2000). Defining a species as ‘invasive’ can be difficult, particularly where spatial patchiness hides a greater system-level effect. The conceptualised process of plant invasions as described by Richardson, et al.,(2000) has three key stages: i) Introduction- The plant has been transported over a major barrier to a novel ecosystem. ii) Naturalisation- Abiotic and biotic barriers to survival have been overcome and regular reproduction is carried out. iii) Invasion- introduced populations must produce reproducing offspring in areas distant from the initial introduction site (Fig. 1). For a species to be considered invasive, Richardson et al. (2000) define the approximate distance scale as >100m over <50 years for seeding taxa and >6m over 3 years for taxa spreading by stolons/vegetative growth (Richardson, et al., 2000).

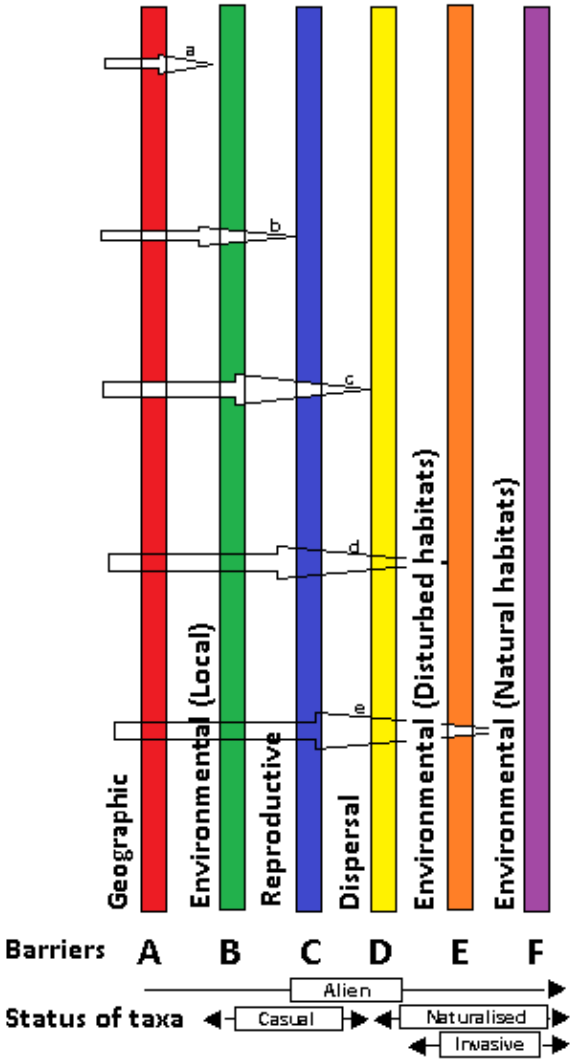

Figure 1.1 Representation of major barriers to the spread of introduced plants.

(A) Major geographical barrier (>100km); (B) Environmental barriers (abiotic or biotic) at introduction site; (C) Reproductive barriers (vegetative or generative); (D) Local dispersal barriers; (E) Environmental barriers in human or alien-disturbed habitat; and (F) Environmental barriers in natural or semi-natural habitats. Adapted from Richardson et al (2000)

1.1.2 Range expansion and rate of spread

Range expansion has close links to invasion biology and is often the most obvious impact metric of an exotic species (Parker, et al., 1999). When a species has fulfilled the three key stages and become invasive, its spread within the new environment (range) and the time scale of this expansion is a function of the species reproductive rate and dispersal characteristics

(Mack, et al., 2000, Sakai, et al., 2001).The influence of various environmental factors on range expansion is also linked to the stage of invasion a species has reached (Dietz and Edwards, 2006). The ecological and evolutionary pressures that affect a species at the start of its invasion change as the species establishes and the invasion progresses. It is therefore critical to identify which stage the invasion is likely to be at, in order to accurately assess the factors affecting its dispersal (Stohlgren, et al., 1999)

1.2 Factors influencing invasion success

Understanding the range and effect of invasions is a major challenge in environmental management and invasion biology (Reichard and Hamilton, 1997, Heger and Trepl, 2003). Predictions of invasion success are often based on the characteristics of the invader and the physical and biological structure of the receiving environment (Huston, 2004). Mortality rates are primarily stress-related, expressed through two processes, abiotically generated stress through extreme conditions or resource scarcity, and biotically generated stress from competition (Davis, et al., 2000; Alpert, et al., 2000). Environmental disturbance acts to vary the relative effect of stress on mortality rates, resulting in altered population survival and species richness (Huston, 2004). Environment type also influences the type of stresses, abiotic stress is typically associated with less productive, dryer environments due to low numbers of competitors. In contrast, biotic stress is generally greater in more accommodating, wetter environments where competition is more intense from dominant species reducing resource availability (Grace, 1999).

1.2.1 Abiotic factors

Without exception, natural environments display gradients, local phenomena and heterogeneity of influences. Abiotic factors (topology, climate, geology etc.) create spatial

variation in biological systems which can be expressed as variations in fitness of local biota (Sexton, et al., 2009). The effect of abiotic factors on plant performance is a contentious issue: there is a well-established school of thought in ecology that predicts invasive species should perform poorly compared to endemics when the endemic diversity is high (Tilman, 1997). Most of the studies addressing this question focus on the biology of the invasive and native species (Shea and Chesson, 2002; Kolar and Lodge, 2001; Daehler and Carino, 2000). Some lend weight to the idea that more diverse communities should be more resistant to invaders (Levine, 2000; Kennedy, et al., 2002) however the general body of evidence contradicts this idea (Shea and Chesson, 2002; Huston, 2004). An alternative to this model assumes that the properties of the physical environment affect species performance (Alpert, et al., 2000). The basis of this second approach is that invasive species respond essentially identically to native species in response to environmental conditions (Huston, 1994).

Discarding the contention that high-diversity communities have higher invasion resistance in favour of an approach based purely on the physical environment may be of value. The argument is ongoing however, and there is a risk of losing important information by disregarding the local biota. Therefore, this study will address the effects of both the physical environment and primary neighbour species.

1.2.2 Neighbour interaction

Interactive relationships may rise from the need of both parties to obtain the greatest material advantage both in terms of single resources and simultaneous acquisition of multiple resources (Aschehoug, et al., 2016). Such interactions can result in complex influence/influencer webs

on an inter-specific and community level (Aschehoug, et al., 2016). Gradients of environmental stressors produce changes in species interactions between favourable and unfavourable environments, resulting in a progression from facilitative interactions to competitive interactions (Callaway and Walker, 1997). Most evidence for competition comes from low-stress/high productivity environments; the more productive environments produce greater biotically generated stresses as most species grow well, but the largest and fastest-growing species exclude poorer performers. (Huston, 2004; Holmgren, et al., 1997). Facilitative interactions such as shade from canopy plants permitting the establishment of new species are more common in harsher environments (Holmgren, et al., 1997).Complex interactions between facilitation and competition due to multiple drivers including stressors, community composition and population demography influence plant community structure (Callaway and Walker, 1997).

1.2.3 Seed bank dynamics

Soil seed banks, i.e. the storage of viable seeds in the soil (Gioria & Pysek, 2015) allow for the establishment of new populations after dispersal, often for many years later. Seed banks play a major role in species succession, particularly in disturbed environments. Many weed species form seed banks, and they are a significant source of invasive populations; Kropac (1966) estimated the potential seed bank of weed flora in agricultural regions to be 39.8-140.6 million per hectare. A common strategy of vegetatively reproducing invasive plants is exploitation of openings in otherwise inhospitable areas, such as light gaps in canopies (Kanno and Seiwa, 2004; Wang, et al., 2013; Hara, et al., 2004; Matlaga and Horvitz, 2009). This trait permits opportunistic expansion into disturbed areas before native cover that would otherwise crowd out the invasives before they can fully recover. It is of particualar value when control

techniques remove biomass but do not prevent regrowth (ie. mechanical clearance). Description of seed bank dynamics and invasive plant species seed persistence within the seed bank is important to invasion biology and conservation, as it will highlight the potential regrowth characteristics of an invader and help predict how long the source of propagules will continue in the absence of further introductions (Gioria and Pysek, 2015). Understanding seed bank dynamics may also inform potential methods of preventing invasions through manipulating seed bank content (Guido, et al., 2017)

1.2.4 Species characteristics

Invasive plants typically have small seeds, short juvenile periods and high output of clonal fragments (Hayes and Barry, 2008). History of invasiveness and vegetative reproduction are strongly associated with invasion potential in novel environments. (Daehler and Carino, 2000) However these are only general assumptions of plant invasiveness, species-level characteristics are regarded as more likely to be taxa-specific (Sakai, et al., 2001).

1.3 Summary

A fundamental concept of invasion biology is quantifying the extent and limitations on range expansion and the reproductive strategy of the invader. This study aims to quantify the extent of *Erythranthe guttata* in a subset of river valleys on Banks Peninsula, New Zealand and identify factors influencing its presence. Exploring the behaviour of this invasive weed is critical to its management within the region and has wider implications for pest control and population research in general.

Understanding of the ecological effect of invaders has a quantifiable impact not only on the general body of academic literature, but also within the wider public; denialism of the negative

effects of invasive species originating from vested interest groups frequently downplays the threat posed by invasive species (Russell and Blackburn, 2017). The needs of invasive species management policy (such as restrictions on species transportation, sale and the policing of same) are often difficult to justify in the face of denialism, particularly given that uncertainty is a natural component of scientific research (Ceccarelli, 2011). An important backstop to policy decisions therefore is robust, empirical studies highlighting the impacts of invasive species and presenting an evidence-based case for management decisions in the arena of public debate.

1.4 The study species, *Erythranthe guttata*

Figure1.2 Erythranthe guttata, (Fisch. ex DC.) G.L. Nesom.

1.4.1 *Erythranthe guttata* biology

Erythranthe guttata, (Fisch. ex DC.) G.L. Nesom, formerly known as *Mimulus guttatus* (Barker, et al., 2012), common name Monkey Flower or Monkey Musk (Barker, et al., 2012) is a perennial herb of wet areas in the family Phrymaceae, order Lamiales. It typically grows between 10 to 80cm tall with large, bright yellow tubular flowers (20-40mm long). The flowers have distinctive lines of rod dots within the corolla and a thick, stiff stem. The flowers dry and detach towards the end of the growing season and the fruiting bodies dehisce, releasing numerous tiny black seeds (0.02g). The leaves vary from obtuse to narrowly ovate with longitudinal venation and display regular serrations that may be smooth-edged or finely dentate. It is a native of western North America where it inhabits an extensive range from Southern California to Alaska in lowland to montane regions (Grant, 1924). Two major ecotypes have been identified in its native range; annual and perennial. The annual populations inhabit hillsides and rocky areas with cyclic dry and wet seasons through the year. Perennials are limited to areas such as borders of waterways and swampy areas with no strong 'dry' period (Lowry, et al., 2008). *E. guttata* is ubiquitous throughout New Zealand from sea level to montane regions and grows vigorously in drainage ditches and rivers.

1.4.2 Introduction to New Zealand

Erythranthe guttata was first introduced to New Zealand in the 19th Century as an ornamental cultivar, the first wild example being collected in the 1940's. *E. guttata*'s biology in New Zealand is like that of its home range and has a near identical ecological niche. The first introduction of *E. guttata* to New Zealand was recorded in 1878 as an ornamental species (Webb, et al., 1988), primarily from European cultivars. Webb, et al. (1988) only note the date of first introduction, not the location. The first instance of a wild specimen was recorded in

Wanganui in the 1940s (Landcare Research, 2014). The actual source of wild populations is not entirely clear; cultivation has been shown to drastically increase the likelihood of successful establishment of escaped populations from even small introductions (Mack, 2000), so original source may have been the demand for ornamental *E. guttata* cultivars or accidental cultivation through crop seed contaminated with seeds (Mack, 2000) Contaminated farm equipment, animals and imported soil-bearing items could be responsible as the seed is readily transported by animals (Vickery, et al., 1986). Pyšek et al., (2011) conclude the greatest likelihood of introduction of an alien plant lies on the source with the highest human involvement and facilitation, in this case the most supported source is commercial cultivars.

1.4.3 Threat to NZ native species

Erythranthe guttata is ubiquitous in New Zealand and is an opportunistic invader that will cover river beds and banks with a thick layer of clonal stems. Its threat to indigenous species comes primarily from smothering competitors with its quick-growing stolons at ground level and tall shoots blocking out light to lower growing plants. Additionally, patches of *E. guttata* can quickly clog agricultural waterways leading to flooding which then requires expensive mechanical or chemical pest management to resolve (Truscott, 2007). 16 of New Zealand's wetland vascular plant species in Conservation Category A and B (Molloy and Davis, 1994) are threatened by weed encroachment (Dopson, et al., 1999).

As *E. guttata* has the potential to rapidly invade riparian habitats, it poses a serious risk of profoundly altering delicate ecosystems and increasing pressure on already endangered native species. Riparian systems are particularly vulnerable to invasive alien plants due to their inherently high frequency of severe disturbance events (Richardson, et al., 2007). Direct drivers of species decline are well developed in the context of alien species; Competition and

density effects (Gooden, et al., 2009) as well as habitat and mutualism effects and interactions between multiple drivers (Downey and Richardson, 2016) can have impacts ranging from species to ecosystem level. *E. guttata* is known to produce a prolifically invasive hybrid with *Erythranthe luteus* (*Mimulus x robertsii*) (Vallejo-Marin and Lye, 2013) however neither this nor any other *E. guttata* hybrid has yet been identified in New Zealand (Landcare Research, 2017).

As yet, *E. guttata* is not listed as a pest plant in the most recent (2008) Christchurch City Council Biodiversity strategy (Christchurch City Council, 2008). This lack of management visibility is of concern given the previously stated damage potential of this weed on riparian ecosystems and native biota. In terms of direct impacts on riparian communities, Truscott, et al. (2008b) note a significant negative effect of *E. guttata* on the richness of local plant species in disturbed habitats even at low relative densities. While Truscott, et al. (2008b) state the threat of *E. guttata* to be primarily towards ruderal plants and non-native weeds in disturbed habitats and conclude little need to manage the species, the study of this invasive weed in New Zealand is limited; further research is critical to developing an accurate threat profile.

1.4.4 Mode of reproduction

Erythranthe guttata's primary reproductive output is through clonal fragments (Truscott, et al., 2006) , most commonly during the October-March growing season. Fragments have a high establishment rate (95%) and waterway transport is the main source of downstream population establishments (Truscott, et al., 2006). Clonal growth produces creeping stolons which establish floral ramets which separate from the parent plant when the stolon dies. Ripe fruiting bodies desiccate towards the end of the growing season and dehisce, releasing abundant seeds when shaken. Seeds typically range between 3-5mg, and 200-500 per capsule. Seed size, seed

number and ability to self, show significant potential for selective variation (Robertson, et al., 1994) . While sexual reproduction may appear unnecessary as a dispersal strategy, this may not be the case. While the small seed size, short range wind dispersal range (Vickery, et al., 1986) and the poorer performance of seedlings in comparison to ramets under shade stress than fragments (Hewitt, 1998) indicate that seeds are likely have little role in reproduction, this may not be the case. Seeds may be an important dispersal strategy, in particular where ramets cannot reach, such as shade gaps in the canopy, as has been noted for the understory shrub *Hydrangea paniculata* (Kanno and Seiwa, 2004) which has similar seed characteristics to *E. guttata.*

1.4.5 Presence in Banks Peninsula

In surveys prior to the starting of this study, profuse populations of *E. guttata* were identified in many streams and ditches alongside the road network of the Herbert and Akaroa administrative regions of Banks Peninsula (Kerr, unpublished data). Minimal populations were also identified in the northern side of the peninsula; however, these were generally in urbanised drainage networks rather than river valleys proper. Historical records of *E. guttata* spread in the area are somewhat limited; in his study of the Banks Ecological region for the Department of Conservation (DoC) in the late 1980's, the renowned Banks Peninsula naturalist Hugh Wilson described populations of *E. guttata* in Dan Rogers creek (Akaroa), Motukarara wetlands and Robin Hood Bay (Wilson, 1992). Additionally, herbarium specimens have been taken from Port Levy (1966), Okuti valley (1967), Akaroa (1971) and Paua Bay (1980) (Landcare Research, 2014 and 2017). *E. guttata* has also been identified in major South Island and North Island catchments in 18% of 62 0.25-1km sections of riverbed (Williams and Wiser, 2004)

1.5 The study site, Banks Peninsula

Banks Peninsula is a volcanic protrusion on the eastern edge of the Canterbury Plains. Historically covered in dense bush in pre-human times, it has now mainly been converted to tussock grassland, rough pasture and forestry blocks. The peninsula has two major natural harbours; Lyttelton and Akaroa, to the north and south respectively of a low mountain range, divided at the highest point by Mt Herbert (919m). Lyttelton harbour was formed within the caldera of the extinct volcano that makes up the majority of Banks Peninsula. Climatic conditions vary considerably across the region; the northern half of Banks Peninsula is comparatively much dryer than the southern half and receives greater sunlight hours due to the northerly aspect of the crater rim. Numerous (~100) small, high gradient waterways run to the sea through dozens of valleys separated by rocky bluffs (Winterbourn, 2008). Due to clearance of land for use as sheep pasture, relatively little of Banks Peninsula has significant tall plants or trees down to sea level. Tree and shrub coverage typically begin to make a significant appearance much closer to the top of valleys. The exceptions in the context of the area studied in this thesis are Mt Vernon, (where a small forest reserve sits at the mouth of the valley which is grassland the rest of the way up to the crater rim) and Hinewai, which is fully regenerated native bush from the ridgeline to a property boundary approximately 100m from the coastline. I chose locations for my study within six geographically distinct areas:

- Sumner Valley- Bush/developed grassland
- Mt Vernon- Tussock grassland
- Orton-Bradley Park- Non-native forest/Native bush
- Kaituna Valley- Developed grassland/Native bush
- Te Oka Valley- Regenerating bush/Un-developed grassland

- Hinewai Reserve- Fully regenerated native forest (bush)

1.6 Aim and structure of this thesis

1.6.1 Overall aim

The overall aim of this thesis is to outline the factors limiting and facilitating the spread and performance of the invasive riparian weed *Erythranthe guttata* in Banks Peninsula, New Zealand. To understand the factors influencing *E. guttata* spread I have conducted two field surveys at a one-year interval, and two glasshouse experiments to test the results of the field data. The two glasshouse experiments consisted of an experiment in two parts testing *E. guttata* performance under varying shading and neighbour species conditions, and a seed bank germination experiment also in two parts. Determination of the factors limiting invasion will improve understanding of the ecology of the species in the context of the Banks Peninsula region and inform conservation decisions around this weedy invader.

1.6.2 Thesis outline

This thesis consists of four primary chapters. The following three chapters will cover the one field and two greenhouse experiments; the field surveys, seed bank and shade/competition experiments. The last will combine the results of the previous chapters, draw conclusions and discuss their significance in the context of the ecology and management of *E. guttata* in New Zealand.

Chapter 2

2. Factors influencing *Erythranthe guttata* distribution and density

2.1 Introduction

Biological invasions are characterised by a remarkable range of spatial and temporal dynamics, the result of complex abiotic and biotic drivers of range extension. International commerce and regional transport infrastructure (e.g. roads, rivers and canals) facilitate the spread of introduced organisms and increase their capacity to colonise geographically diverse habitats (Sakai, et al., 2001; Pysek and Hulme, 2005). Understanding the factors behind landscape-level characteristics such as rate of spread and persistence of potentially invasive taxa is critical for early detection, accurate monitoring and development of potential control measures (Foxcroft, et al., 2007; Pheloung, et al., 1999; Tucker and Richardson, 1995), as well as developing models to predict dispersal (Wadsworth, et al., 2000; Foxcroft, et al., 2007)

Erythranthe guttata is absent from the Ministry for Primary Industries Unwanted Organisms Register (Ministry for Primary Industries, 2019). While it is not officially recognised as a threat, it poses a potentially serious risk to the native riparian flora of New Zealand. Elsewhere it has been shown to display several traits associated with invasive species- effective long/short range dispersal (Truscott, et al., 2006; Grime, et al., 1988), rapid germination (Elderd and

Doak, 2006) and high (~50%) overwinter seed survival rate in its home range (Elderd and Doak, 2006). Moreover, in New Zealand, on the Canterbury Plains, it is an able invader, and rapidly grows in dense patches that can completely smother large patches of riverbank (Collins, et al., 2018). *E. guttata* can colonise a wide range of waterlogged habitats, from agricultural drainage ditches to seeps in rocky outcrops and boggy regions of farmland (Grant, 1924).

Riparian ecosystems are considered especially vulnerable to invasion (Truscott, et al., 2008; Richardson, et al., 2007). For example, river floors are easily invaded, possibly because floods disturb the native vegetation, opening up habitat to invasive taxa (Hood and Naiman, 2000). Moreover, rivers provide potential for waterborne transport of invasive propagules. The same arguments apply to human channelisation activity, rather than flooding events (Aguiar, et al., 2001). Sixteen of New Zealand's wetland vascular plant species in conservation Category A and B (Molloy and Davis, 1994) are threatened by weed encroachment (Dopson, et al., 1999).

Various hypotheses exist to account for the temporal and spatial dynamics of invaders (Pysek and Hulme, 2005, Bradley, et al., 2011, Heger and Trepl, 2003). These focus primarily on the characteristics of the invasive species, while analysis of the effect of host environment on invasive success is often broad-scale and limited to range expansion within disturbed or degraded habitats. However, assessing dynamics of range expansion on a granular scale within a geographic zone provides context to broader studies across a wide range of environments (Hulme, 2006). Broad-range studies may overlook important small-scale variation (Truscott et al 2008a), studies of small plots have proven to be of value in assessing invasion dynamics, for example Stohlgren, et al., (1999).

Truscott et al (2008a) explored the influence of several biotic and abiotic factors on *E. guttata* occurrence and abundance (as measured by number of patches, patch area and number of stems per patch) in riparian habitats in Scotland. They studied ~700 contiguous 50-m stretches of river in the Tarland catchment in north-east Scotland, recording their biotic and abiotic characteristics and collecting *E. guttata* occurrence and abundance data. Their results showed that occurrence and number of patches were associated with the same environmental variables (See table 2.3). Patch area and number of stems per patch were associated with a somewhat different set of environmental variables (Table 2.3). Given these findings, Truscott et al (2008a) highlighted the need to consider multiple measures of invasion success (i.e. multiple measures of abundance such as stem number per area as well as occurrence data) and ecosystem-level characteristics of invaders as spatial heterogeneity and 'patchiness'. Other studies have also concluded measures of invasion based on a single measure of species performance, such as abundance, can be unreliable. For example, Stohlgren, et al. (1999) and Cross, et al., (2017) found significant variation in the factors influencing occurrence versus abundance of invasive species. Cross, et al. (2017) conclude that occurrence alone is an unreliable predictor of invasive plant abundance.

The duration of the study is also an important factor: a meta-analysis of 410 papers examining the ecological impacts of biological invasions between 1971 and 2011 by Stricker, et al. (2015) identified that 51% of studies examined were of less than a year's duration. Previous studies have identified the need for evaluations at varying temporal scales (Parker, et al., 1999; Stricker, et al., 2015). Additionally, Stricker, et al. (2015) found the clear majority of

observational studies were of less than a year's duration and consisted of a single observation event. Following the recommendations of Truscott, et al. (2008a), Stricker, et al. (2015) and Parker, et al. (1999), adding a second survey at a year's interval has potential to improve the reliability of the conclusions reached by this study.

2.1.3 Summary

Studies on a fine spatial scale, incorporating several different measures of a species occurrence and abundance may have potential to uncover effects and trends that would otherwise be overlooked in studies on a broader scale. Multiple measures of invasion (number of patches, patch area, number of stems per patch etc.) in addition to occurrence, are of value in studies of how invasive species react to environmental factors, as they capture a more nuanced picture than those merely focusing on occurrence. Adding a temporal dimension to these studies has been identified as being of importance in assessing which factors are influencing measures of invasion success.

2.1.2 Objectives

My first objective in this chapter is to determine the influence of key biotic and abiotic factors influencing the spread of *Erythranthe guttata* on Banks Peninsula, New Zealand. My second objective is to assess whether these factors are consistent between years, in order to detect whether other, unidentified factors may be influencing abundance and occurrence. My third objective is to look for evidence of *E. guttata* range expansion within the locations I surveyed, and if such expansion exists, to discuss whether it is sufficient to consider it invasive.

2.2 Method

2.2.4 Study locations

My surveys were conducted along six river valleys across Banks Peninsula. I based my choice of river valleys on published GIS land coverage data (Land Information New Zealand, 2018) which I used to produce a shortlist of 12 valleys which together were representative of habitat type, aspect, vegetation coverage and topography of the Peninsula. Of these 12, my final choice of six locations was determined by feasibility of data collection- in particular, key considerations were road access and ability of streams to be navigated on foot were key considerations, as my data collection was entirely carried out by walking along, and often in, the rivers.

The final six geographically distinct river valleys I used in my study are presented in Table 2.1 and Figure 2.1. Each of the six valleys represents a distinct habitat type within Banks Peninsula and the six habitat types are broadly representative of the whole region's highly diverse geography.

Location	Habitat type
Sumner Valley (SUM)	Bush/developed grassland (Bush/DG)
Mt Vernon (MTV)	Tussock grassland (UDG)
Orton Bradley Park (OB)	Non-native forest (F)
Kaituna Valley (KAI)	Developed grassland (DG)
Te Oka Valley (TOK)	Regenerating bush/UDG (Bush/UDG)
Hinewai Reserve (HIN)	Fully regenerated native forest (Bush)

Table 2.1 Study locations and habitat types

(abbreviations used in text in brackets)

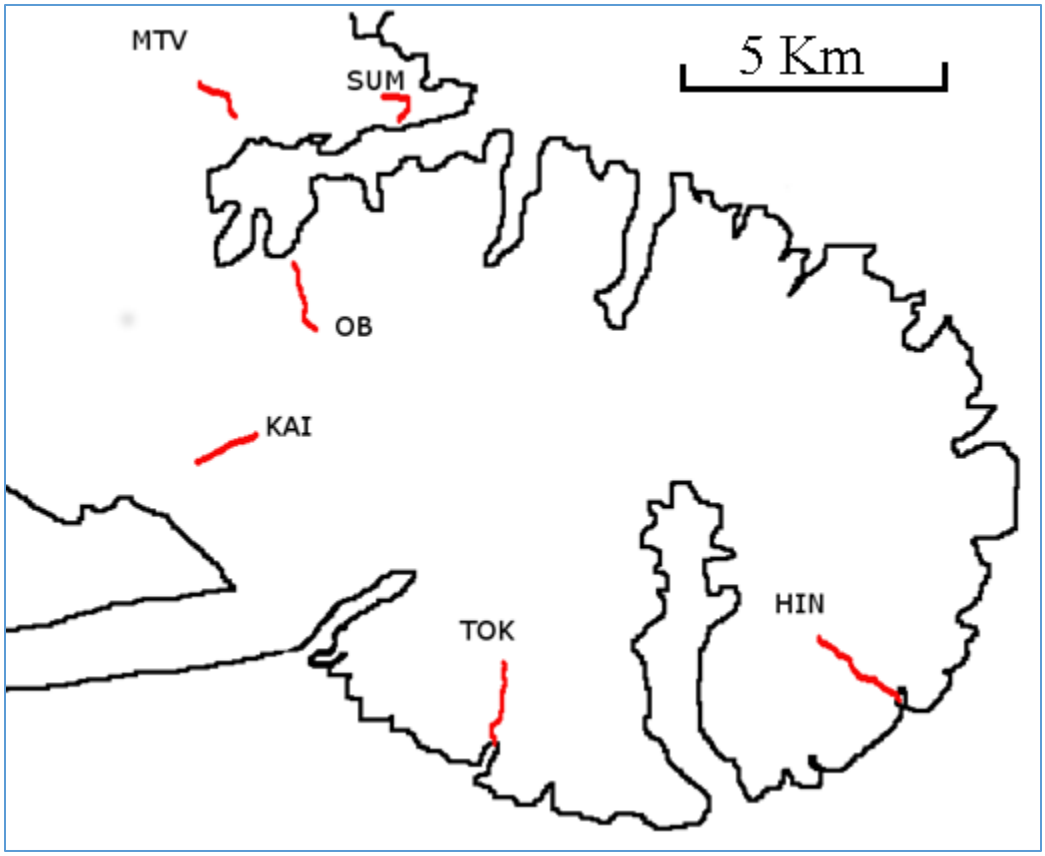

Figure 2.2 Outline map of Banks Peninsula area.

Names abbreviated as in Table 2.1, Study locations are in red.

I visited each location in September-October of 2017 to confirm suitability and again in November 2017 to conduct a preliminary walk-through of the stretch of river I proposed to survey. In this preliminary survey I noted site characteristics, including aspect, human activity and land use for future reference.

2.2.5 Survey method

I carried out the first detailed survey over January to late February of 2018, during the *E. guttata* flowering season. The survey consisted of 221 contiguous 50-m sections (sites) of river within the six river valleys (Table 1). At each site I recorded its GPS location at each end and measured nine environmental characteristics based on Truscott, et al. (2008a):

- Shading intensity

  I estimated shading using a method adapted from Hanh and Scheuring, (2003) and Anderson, (1985). I visually divided the area under investigation into ten equal parts, five each side of the river. Shading was then estimated using a nearest 10% except at the high end (80%+) of the scale where units of 1% were used, as finer resolution has been shown to be of value in vegetation cover experiments (Hanh and Scheuring, 2003; Onodi, et al., 2017).

- Total area of open sediment patches

  I measured the area of open sediment patches using a ruler, and approximating the square area of each patch. Sediment patches were defined as patches of mud, silt gravel and pebbles without vegetative cover (Wentworth, 1922) following Truscott, et al. (2008a)

- Total number of open sediment patches
- Primary vegetation species (species comprising > 20% of the vegetation)
- Number of trees

  I noted primary vegetation species using a species guide into nine categories (see Appendix 3) and visually counted the number of trees.

- Substrate type

  I classified substrate type into three broad categories; 'Rocky', Rocky/Clay' and 'Clay' using a simplified version of the Wentworth grain size classification scale (Wentworth, 1922). Substrate primarily composed of rocks (4000mm-16mm) was classified as 'Rocky', substrate sand/silt/clay (<2mm to <0.063mm) was classified as 'Clay' and a combination of the two was classified as 'Rocky/Clay'

- Habitat type (See appendix 2)

  I classified habitat type into four broad categories; 'Developed Grassland', 'Undeveloped Grassland', 'Forest' and 'Bush'.

- Height of surrounding vegetation
- River dimensions (total width and depth of water) to give river volume

  I measured height of vegetation and river dimensions using a measuring rod and ruler. Depth was measured using a measuring rod with 10cm graduations, and depth was rounded to the nearest 10cm.

I chose these environmental characteristics based on Truscott, et al. (2008a). At each 50m site I recorded all environmental characteristics at three locations, equally spaced along each 50m section, the average value being calculated afterwards. I measured each section using a pacing method adjusted to the habitat type as described in Cross, (1989), where a standard distance (in this case 50m) is measured using a tape measure and the number of paces to cover the distance are then used as a measure of distance.

Where *E. guttata* was present, I measured four performance estimates:

- 'Stem number' which is the average density of stems per 400cm^2, per 50m segment.

I chose stem number following Truscott, et al. (2008a) as a measurement of *E. guttata* abundance. I have used 'stem density' throughout the text where 'stem number' would be inappropriate for explanation, the two are interchangeable. Due to the high number of stems encountered per patch (one patch was estimated to contain over 100,000 stems, several were estimated at over 6,000) and limited scope of this study, I used average density based on multiple measurements of each patch instead of a census of stems. I measured stem number

using a 20x20cm quadrat, patches smaller than 400cm^2 were not recorded as stem number could not be accurately measured. I decided upon the quadrat size based on plant size, following Jelbert, et al., (2015).

- Number of patches
- 'Total patch area' which is the total area of *E. guttata* coverage recorded per 50m segment.

I chose the number of patches as a measure of occurrence, abundance was measured by patch area and stem number (number of stems per 400cm^2), following Truscott, et al., (2008a). These authors define a patch as a spatially distinct, non-connected area of *E. guttata* stems .They additionally characterise patches as the base unit of population, which is acted upon by environmental factors which influence patch number and size (Truscott, et al., 2008a). I have used this definition throughout.

- Evidence of herbivory

Herbivory has potential to significantly alter population dynamics and overall performance in plants (Palmisano and Fox, 1997). I recorded evidence of herbivory in order to investigate whether plants were being grazed by insect or mammalian herbivores. I checked for leaf and stem damage patterns specific to the type of herbivory in each patch (whole-plant damage by large teeth vs patches of leaf and stem damage). Herbivory was included as an environmental factor but was not included in the analysis as a response category

I photographed three sites in each valley location in the first survey and re-photographed them in the second survey for visual comparison. In addition, I set up nine permanent photographic sites for future research purposes (See Appendix 1).

The sites with identified *E. guttata* populations were re-surveyed in October-November of 2019. All locations with no recorded *E. guttata* presence in the 2018 survey were assessed for evidence of new *E. guttata* populations. Observations of changes to sites such as land slips, moved boulders, fallen trees etc., were taken concurrently. A few weeks prior to the 2019 survey, all bar a 350m stretch of the Kaituna Valley sites were mowed to the waterline; hence this data is incomplete for 2019.

2.2.6 Data analysis

I carried out all my analysis using R 3.3.4 (R Core Team, 2018). I conducted a Principle Component Analysis (PCA) to identify and illustrate the differences in the main abiotic and biotic among the six valley locations. PCA is a tool for reducing a large set of variables into a smaller set while retaining their information and visualises the important variables in a graphical representation to display clusters within the data.

I used an Analysis of Variance (ANOVA) to test for the influence of environmental factors on *E. guttata* occurrence and density. The five environmental factors I included in the analysis were vegetation type, shading, river volume, substrate and habitat type and their interaction. I categorised vegetation into nine types according to the predominant vegetation within each section: fern, flax, tussock, barley, mixed tussock and grasses, *Rubus* species, thistle/nettles and 'other' (See Appendix 3). Shading represents the mean shading intensity per 50m segment. River volume was calculated by multiplying the river width and depth and averaging this value over the 50m segment (Harding, et al., 2009). Substrate represents the underlying riverbed and

river bank type. The interaction between each of these factors is the variation within the six sampling locations for the primary population measures:

i) 'Stem number' which is the average stem density per 400cm^2, per 50m segment.

ii) 'Patch Area' which is the total area of *E. guttata* coverage recorded per 50m segment.

I used a log transformation for *E. guttata* patch area as the distribution did not meet the assumptions of the ANOVA for homogeneity of variance and normality.

I used multiple pairwise comparisons using the Tukey's Honest Significant Differences (Tukey's HSD) test to determine which levels of habitat, substrate and vegetation type differ significantly from each other. This is important as the ANOVA results only tell us which of the variable means are significantly different from the other means. The family-wise error rate of the analysis was α=0.05. The family-wise plots below compare the differences in the mean response variable between pairs of categories (for example, Bush and Undeveloped grassland) to see whether the mean value of the response value in every observation of the first category is significantly different to that of the second category. A positive result means that the first category is positively associated with the response in comparison to the second, and *vica versa*.

2.3 Results

2.3.1 Overall effect of abiotic and biotic site variables among they surveyed valley systems

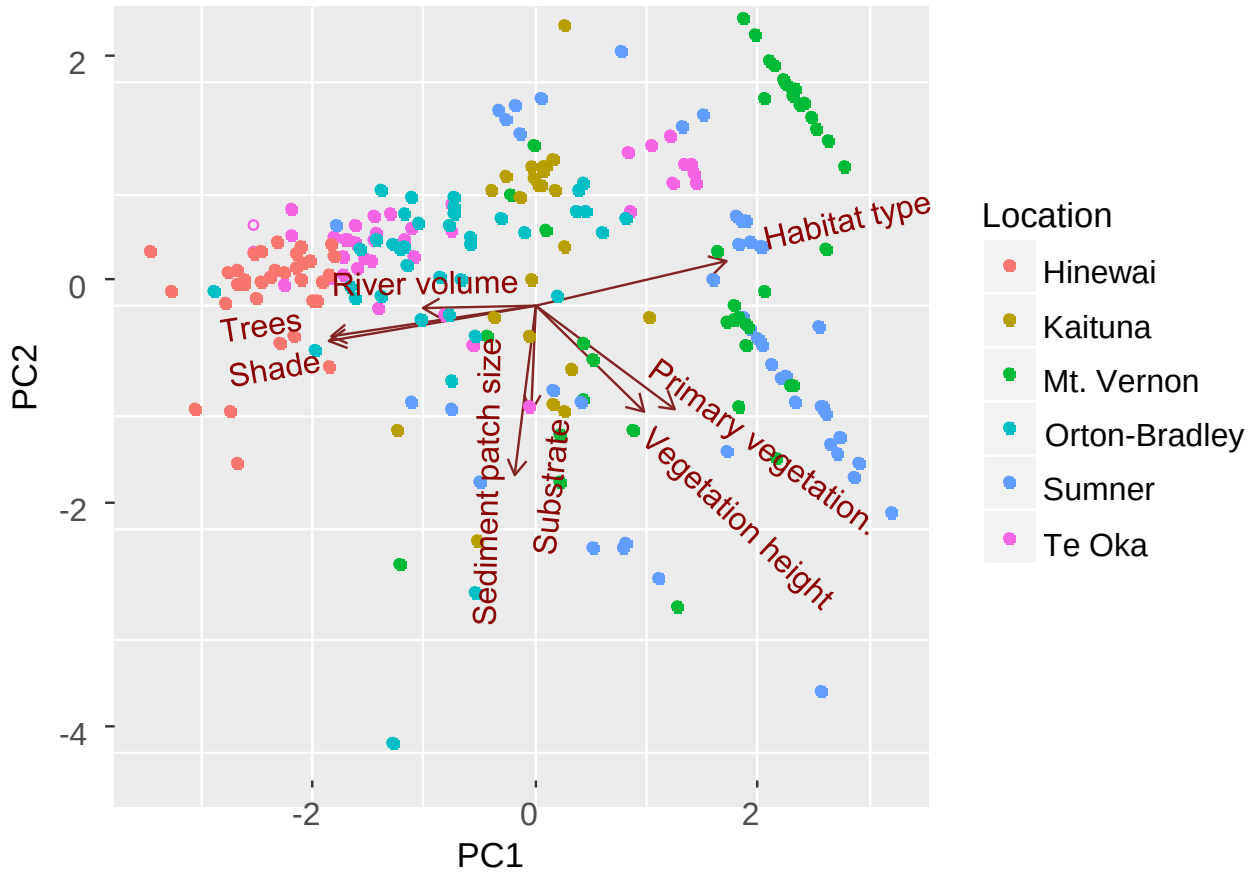

Figure 2.1 Principle Component Analysis (PCA) of abiotic/biotic variables.

PC1 vs PC2 for the 221 50m sections surveyed. Each dot represents a single section of river valley. Colours denote the river valley of the sampled section. 'Trees' represents the number of trees per 50m section. 'Shade' represents shading intensity as a percentage. Modified from Truscott, et al. (2008a)

To identify and illustrate the main abiotic and biotic differences among the six river valleys I ran a PCA on all variables (Figure 2.1). The difference in abiotic and biotic factors among the six study sites is summarised in the PCA plot, site biotic/abiotic characteristics are summarised in Appendix 4**.** The first two axes of the PCA together account for a cumulative variance of 52.8%, of which a third of total variance (37.5%) is explained by PCA axis 1 (vegetation

height). Hinewai and Orton Bradley are located towards the left of axis 1 and stands out as the most forested and shady river valley. In contrast, the most open, dry sites such as Mt Vernon and Sumner are located towards the far right of this axis are the valleys which have the least shading and forest cover. Orton-Bradley, Kaituna and Hinewai have the broadest and deepest rivers.

Axis 2 (river volume) explained approximately half the variation of axis 1 (14.6%) and represents the characteristics of the waterways (i.e. Mt Vernon stream is narrow and ephemeral with minimal sediment vs. Kaituna Valley which has a broad river that takes the runoff from Mt Herbert and has large sediment patches). The other five axes represent more minor environmental variables. Therefore, the major environmental gradients observed are local plant community structure (including vegetation type, vegetation height and number of trees), light availability and local river dimensions and configuration.

2.3.2 Influence of environmental variables on *E. guttata* occurrence and abundance

The key biotic and abiotic factors affecting the four measures of *E. guttata* occurrence and abundance are presented in Tables 2.2 and 2.3.

Variable	*E. guttata* occurrence	Patch no.	Log Patch Area	Avg. Stem no.
Valley	***	***	***	***
Vegetation type	**	*	***	*
Shading intensity	***	***	***	***
Habitat type	**	***	*	
Year	**	***	***	***
Interaction	**	***	***	***

Table 2.2 Summary of key biotic and abiotic factors affecting the four measures of Erythranthe guttata *abundance across both survey years (2018 and 2019).*

Variables are Yes/No occurrence, total patches per 50m segment, Log total patch area per 50m section and mean stem density per 50m section *: <0.05, **: <0.01, ***:<0.001 (blank=non-significant).

All occurrence and abundance measures were strongly positively associated with valley location ($p<0.001$). Shading was shown to have a strong negative association with occurrence and abundance ($p<0.001$). Vegetation type and habitat type (see table 2.2) were also strongly positively associated with occurrence and abundance, albeit less consistently (i.e. Habitat type was not significantly associated with stem no.). Number of trees, river volume, sediment patch number and substrate type were non-significant across all performance measures. Survey year was significant across all performance measures, confirming there is yearly variation in *E. guttata* performance.

Variable	**2018 Survey**				**2019 survey**			
	***E. guttata* occurrence**	**Patch no.**	**Log total patch Area**	**Avg stem no.**	***E. guttata* occurrence**	**Patch no.**	**Log total patch Area**	**Avg. Stem no.**
Valley location	***	***	***	***	***	***	***	***
Shading intensity	***	***	***	***	***	***	***	**
Habitat type	**				**	**		
Sediment patch size	*		*					
Vegetation height						*	*	
Vegetation type	*	*	*			*	***	***
Interaction						***	***	**

Table 2.3 Summary of main abiotic and biotic factors influencing E. guttata measures, by year;

Measurements of *Erythranthe guttata* occurrence are Yes/No occurrence. Measures of *Erythranthe guttata* abundance are total patches per 50m segment, Log total patch area per 50m section and mean stem number per 50m section *: <0.05, **: <0.01, ***:<0.001 (blank=non-significant)

Comparison between years (Table 2.3) shows considerable variation in the significance of the influence of some of the measured variables on *E. guttata* performance between years. In contrast, valley location and shading intensity remained strongly significant in both years.

Habitat type was significant for occurrence measures in both years, more so in 2019. Sediment patch size was sparingly significant in 2018 and non-significant in 2019. Vegetation type was more significant in abundance measures in 2019. Vegetation height showed marginal negative correlation with patch number and area in 2019. The results from both years confirm the consistent influence of shade intensity (and by proxy light availability) on all *E. guttata* performance measures (Table 2.2 and 2.3). That is, shading intensity has a negative influence on measures of occurrence and abundance. The positive effect of open sediment patches on *E. guttata* occurrence that I had expected from the work of Truscott, et al (2008a) was very limited in this study.

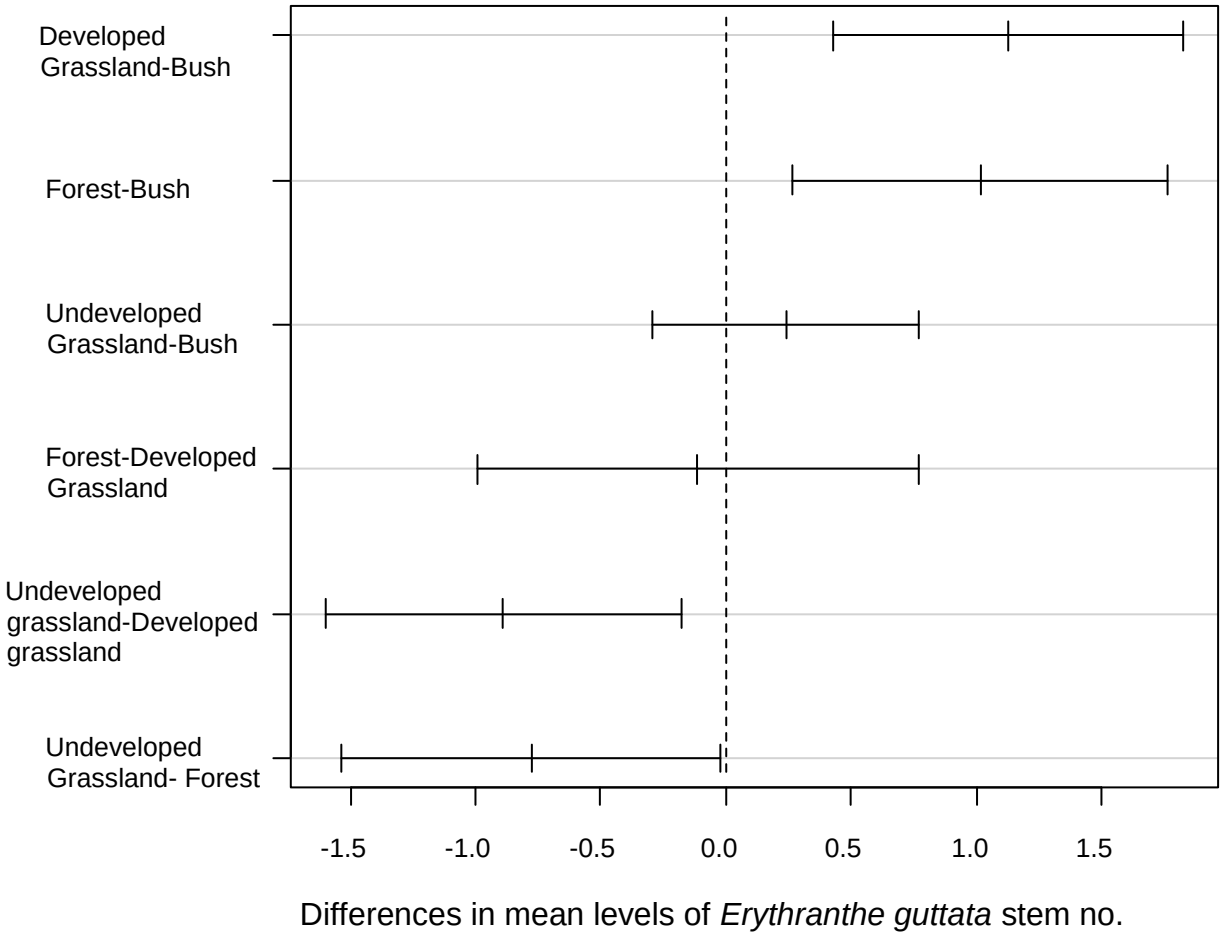

Figure 2.2: 95% confidence interval family wise plots for stem number. Habitat types (y) vs. differences in mean levels of Erythranthe guttata *stem number (x)*

Each horizontal plot line represents the comparison between two substrate/habitat means. The central mark represents the difference between the means, with the outer marks representing the upper and lower confidence intervals.

As a measure of abundance, stem number is used here to compare different habitat types. A positive value indicates that the first habitat is associated with greater stem number than the second.

Stem number was lower in bush habitats (such as Hinewai and areas of Mt Vernon and Sumner valleys) compared to developed grassland and forest (Orton-Bradley and Kaituna Valley). I expected this result as it agrees with the findings of Truscott, et al. (2008a) and the results of the PCA (figure 2.1) which showed that Hinewai has generally lower light

availability. Undeveloped grassland showed no significant difference to Bush and showed lower mean stem number in comparison to developed grassland and forest (Figure 2.2). This was also expected, as much of the habitat in the valleys that had no identified *E. guttata* populations was undeveloped grassland Overall, developed grassland and forest habitats showed greater positive association with stem number.

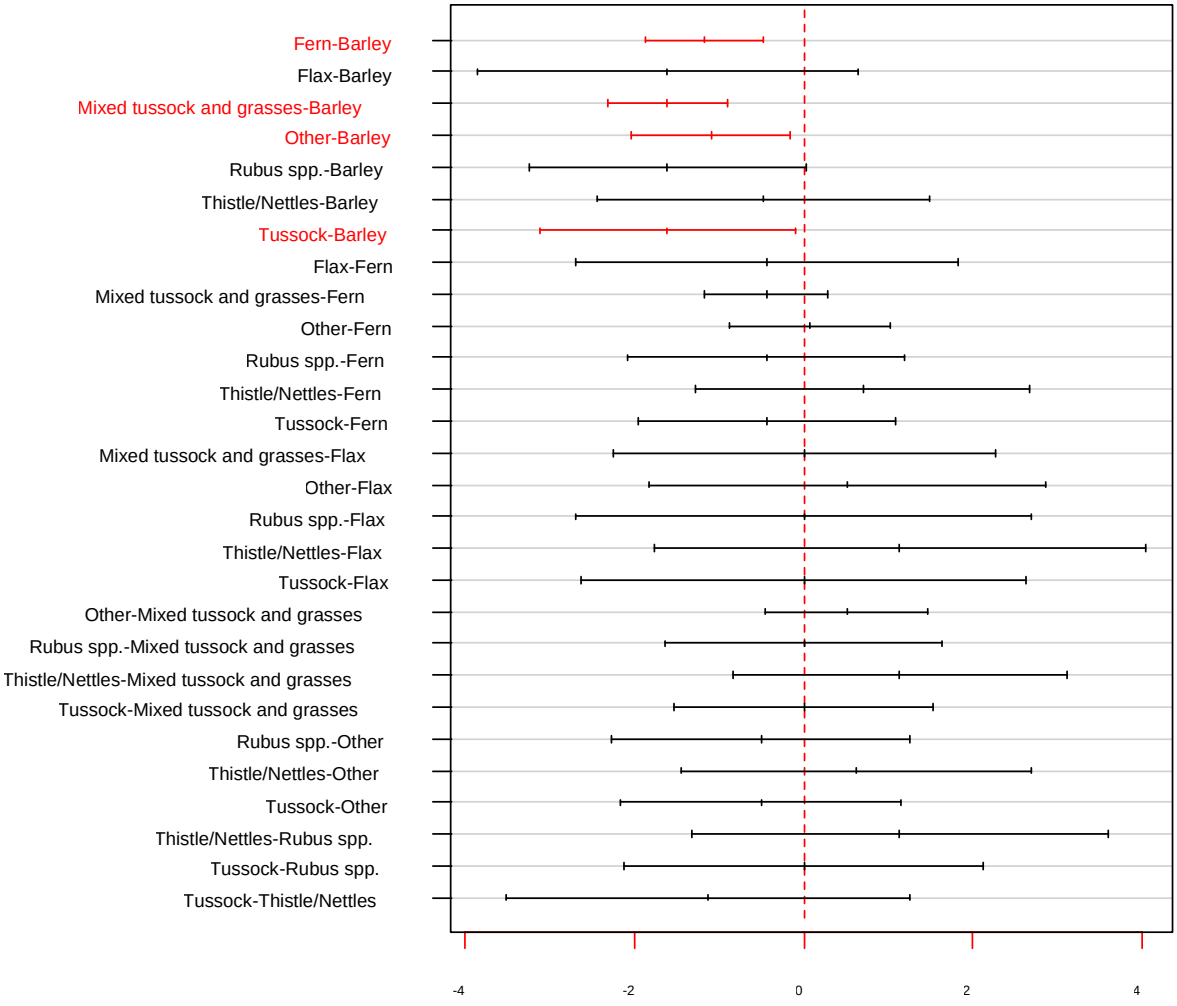

Figure 2.3: 95% confidence level family-wise plot for stem number. Vegetation categories (see Appendix 4) (y) vs. mean difference in Erythranthe guttata *stem number(x)*

Each horizontal plot line represents the comparison between two vegetation type means (significant values are represented by a red line and text). The central mark represents the difference between the means, with the outer marks representing the upper and lower confidence intervals. Significant effects are shown in red.

Neighbouring vegetation species were a significant factor in measures of *E. guttata* occurrence and performance; differences in mean stem number between vegetation categories were significant in all comparisons of barley grass (*Hordeum vulgare*) with all other vegetation types (Fig. 2.3). All other vegetation type comparisons were non-significant (See appendix 2 for a full description of vegetation type classifications). This suggests a potential interactive relationship between Barley grass and *E. guttata*, given that Barley makes up just under half (100) of the observed vegetation types, but accompanies 73% (44) of the observed *E. guttata* populations.

2.3.2 Trends in dispersal & measures of abundance/occurrence across the 2018 and 2019 survey years

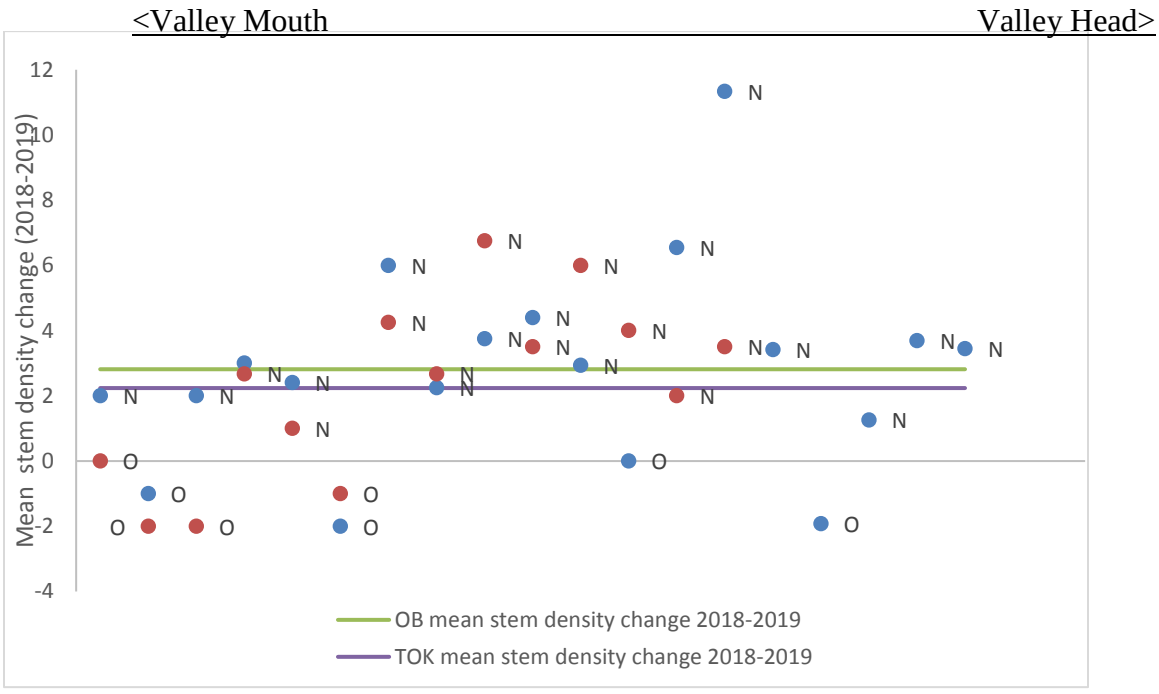

Figure 2.6 Average stem number of 50m sections with identified patches of Erythranthe guttata *in the 2019 survey.*

Each dot represents a 50-m section with an identified E. guttata population; the lines represent the valley mean change between 2018 and 2019. Data point labels indicate whether the section has an old 'O' or new 'N' E. guttata population in the 2019 survey. The x-axis represents the relative position of each section in the valley (Mouth or

Head). The y-axis represents log mean change in E. guttata density between the 2018 and 2019 surveys. Data from Kaituna Valley is omitted due to incomplete records for 2019.

In 2019 I identified the patches of *E. guttata* I had recorded in the 2018 survey and as far as possible recorded new patches. Figure 2.6 shows the mean stem number change for Orton Bradley and Te Oka Valley locations, as well as individual 50m sections from each location with patches identified. The general trend appears to be that most sections with 'old' patches tended to show a reduction in stem density. The distribution of 'new' patches tended to cluster around the middle of the length of river surveyed, with fewer towards the extreme ends. In both valleys, *E. guttata* expanded its range upwards towards the head of the valley, and average stem density increased overall by ~2.0-2.5 per 400cm^2 in the two locations. In Kaituna valley, comparison of the 2018 survey and 2019 data (partially complete, see Methods) showed seven new populations in an area of approximately 350m. The observed overall linear expansion of *E. guttata* was 200m and 400m for Orton-Bradley and Te Oka respectively,

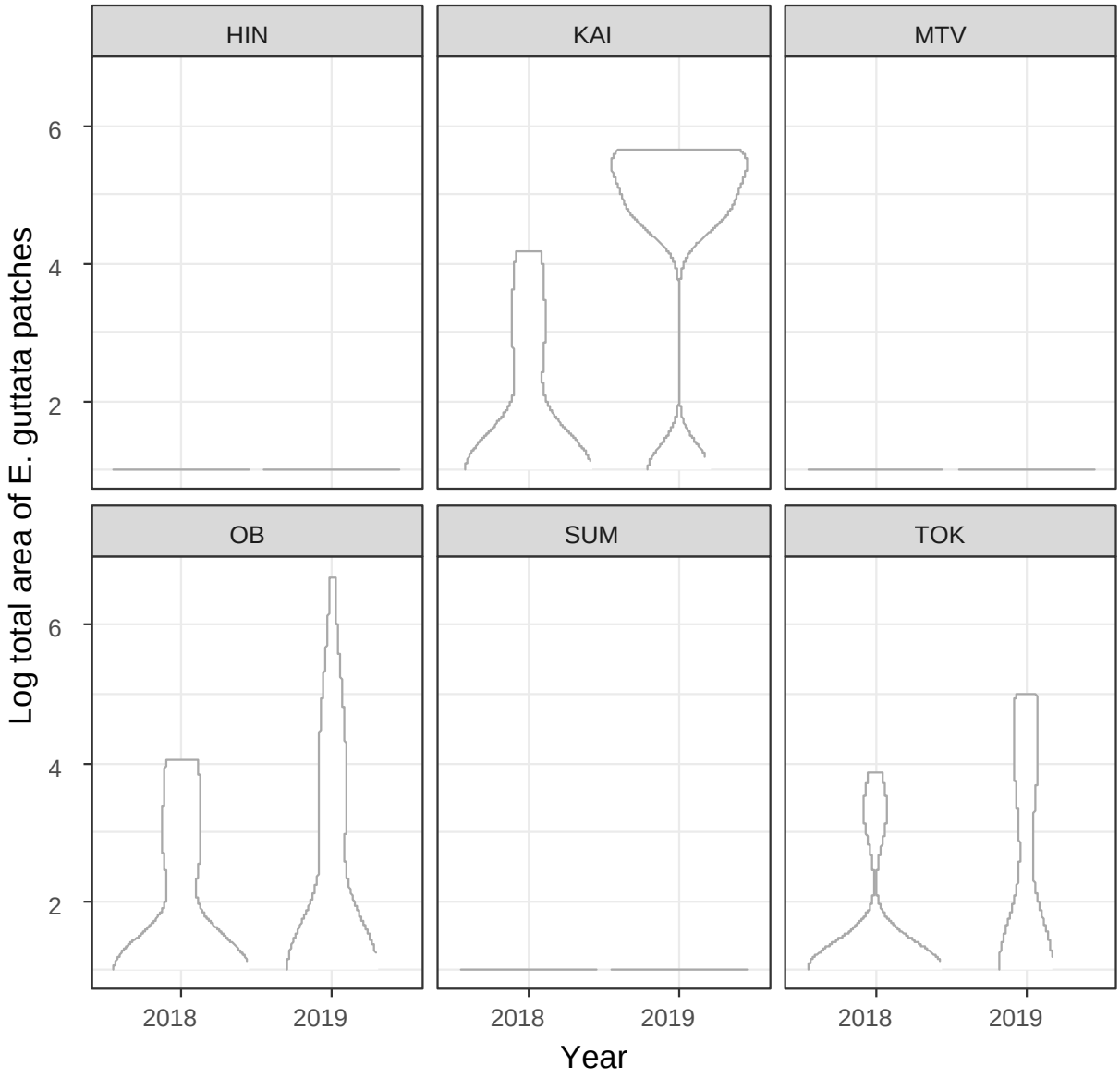

Figure 2.7 Yearly change in log area of Erythranthe guttata *patches, by valley location*

Each section represents a particular valley location, with the associated data from each year (2018 & 2019). Greater relative breadth of the shape represents a greater number of observations at the y-axis level. Log total area represents the log-transformed total area of E. guttata recorded, per 50m section. Location names abbreviated.

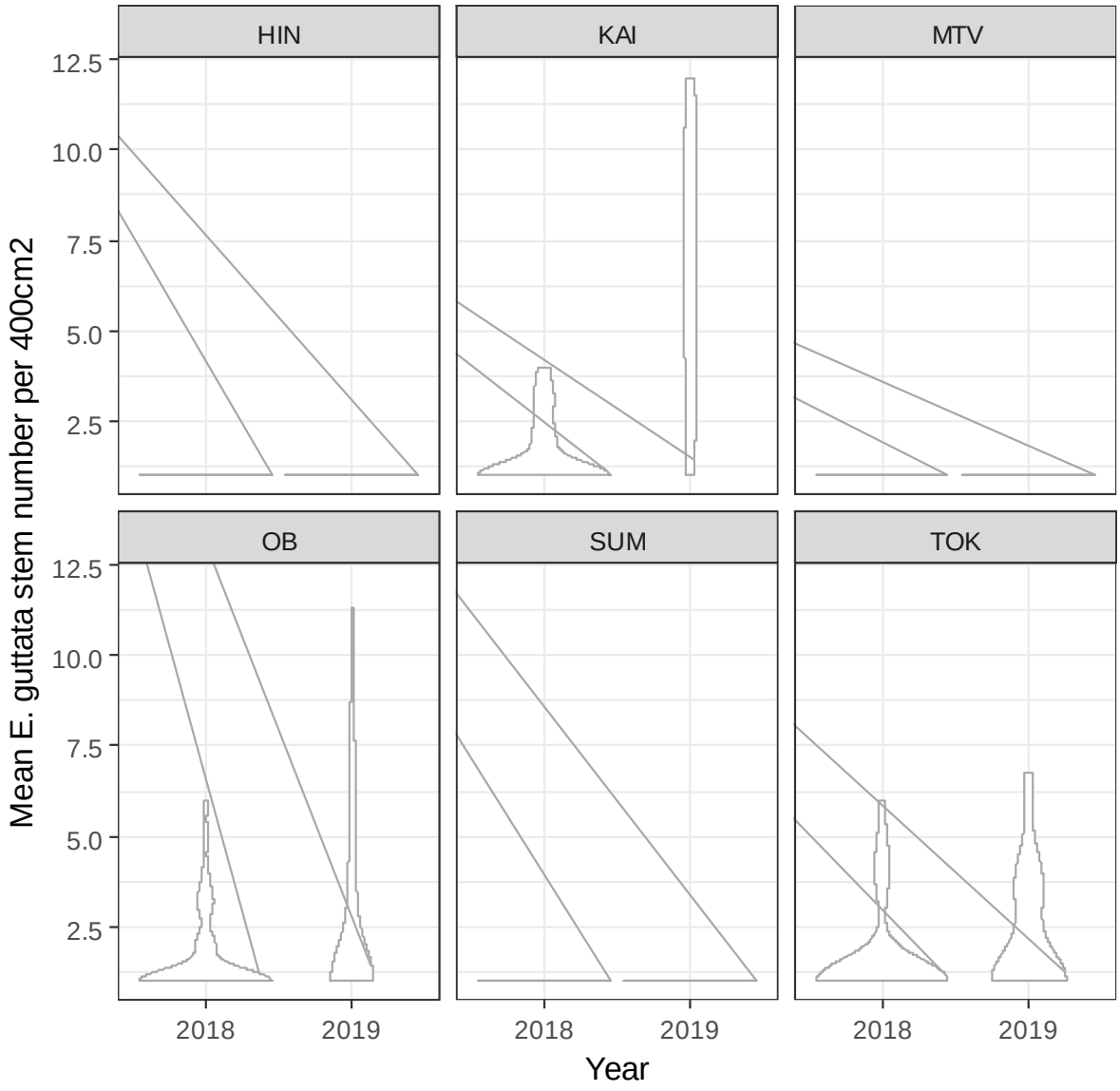

Figure 2.8 Yearly change in mean Erythranthe guttata *stem number, by valley location*

Each section represents a particular location, with the associated data from each year (2018 & 2019). Greater relative breadth of the shape represents a greater number of observations at the y-axis level. Mean stem number represents the average number of separate stems with flowers/fruiting bodies within a 400cm^2 (20x20cm) quadrat for each identified E. guttata patch, per 50m section. Location names abbreviated.

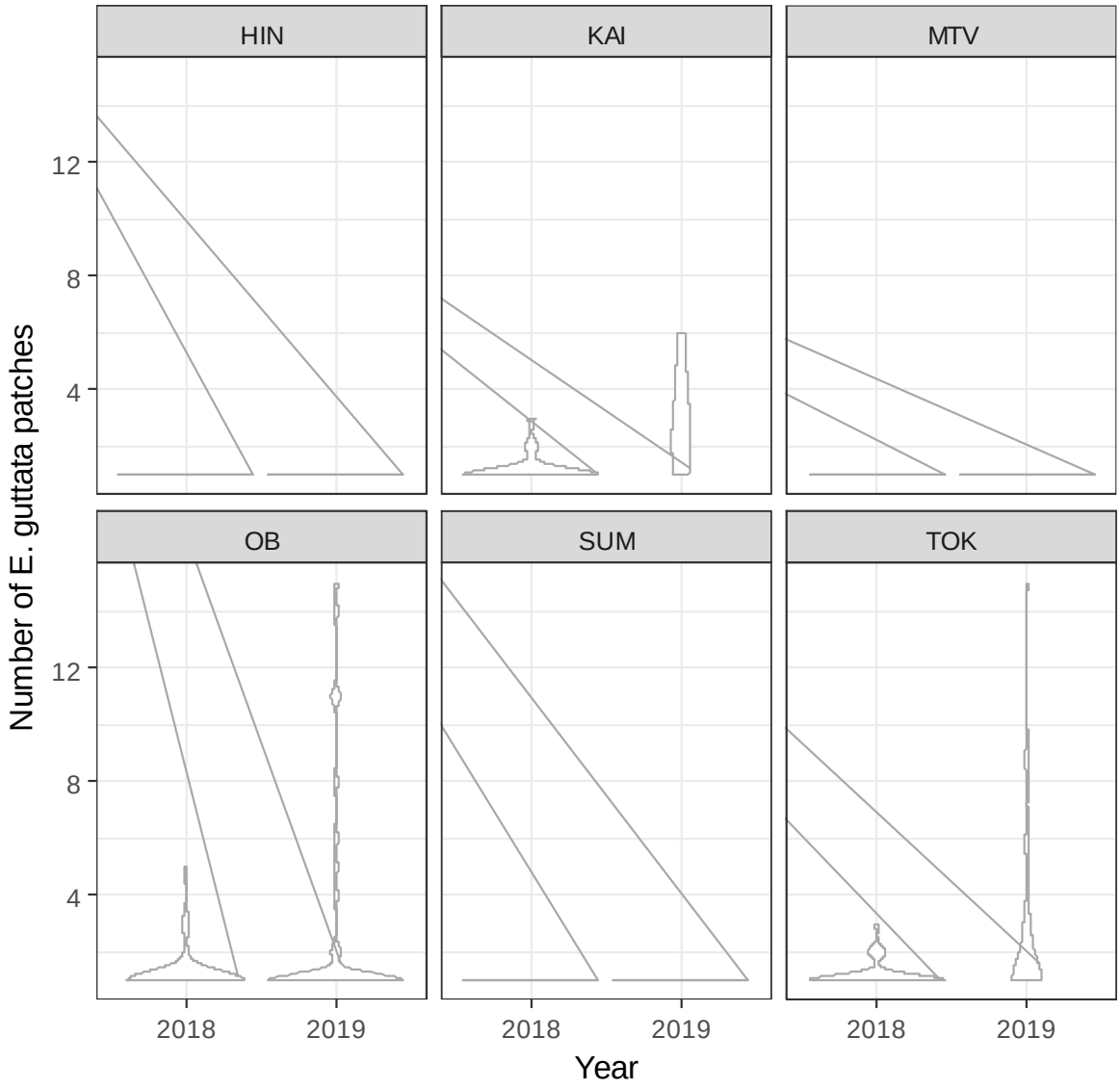

Figure 2.9 Yearly change in number of Erythranthe guttata *patches, by valley location*

Each section represents a particular location, with the associated data from each year (2018 & 2019). Greater relative breadth of the shape represents a greater number of observations at the y-axis level. Number of patches represents the total number found within any given 50m section. Location names abbreviated.

Stem density, total patch area and number of patches per 50m segment all showed increases in magnitude (average values and number of values) in the two valleys successfully surveyed (Figures 2.7-2.9). Kaituna valley also showed similar results in the section that was able to be surveyed. All populations in Te Oka Bay and Orton Bradley increased in total area, linear

spread and mean stem density. The mean linear area increase over all sections with *E. guttata* populations was approximately 275cm (+/-131cm) (assuming roughly square patch layout).

2.4 Discussion

Prior to the 2018 survey, I conducted two preliminary surveys around several river valleys on Banks Peninsula, including the six valley locations included in this study. The purpose was to gather general environmental information on each river valley and assess feasibility of potential locations for study. All valley locations surveyed (n=12) in the southern arm of Banks Peninsula were found to have significant *E. guttata* populations. Additionally, profuse *E. guttata* growth was found along roadways and in ditches in the region. The Okuti and Okana rivers near Little River were considered as a potential study location and would have been included in the survey, however difficulty gaining access to private land along the river bank and potential confounding factors of chemical and mechanical control ruled out this location from the study.

2.4.1 Differences from previous work Truscott, et al. (2008a)

From previous work in Aberdeenshire, Scotland (Truscott, et al., 2008a) and the Canterbury plains (Collins, et al., 2018), it was expected that shade intensity would be a key factor in the occurrence of *E. guttata* in the region. Other biotic and abiotic factors identified as influential on patch occurrence by Truscott et al. (2008) were open sediment patches and lower level ruderal growth. Truscott et al. (2008) included Ellenberg indicator values (Ellenberg, 1988), however these were not appropriate for New Zealand, so I excluded them. Critical differences between the Scotland study location and Banks Peninsula are: different sunshine hours; mean annual sunshine in East Scotland is ~1200 hrs/yr (Met Office, 2018) whereas

Christchurch experiences ~2100hrs/yr (NIWA, 2017). The Aberdeenshire location is primarily arable land (25%) plantation forestry (19%) and improved grassland (36%) (Bergfur, et al., 2012). The Plains Ecological Region and Banks Ecological Region included in this survey are mainly undeveloped grassland with steep, dry ridgelines dividing valleys. Additionally, the high flow rate of the many streams in the region (Winterbourn, 2008) differs significantly from lower flow regimes in the Aberdeenshire and Canterbury Plains rivers.

Variable	**Results from this study**	**Result of Truscott, et al. (2008a)**	**Agreement**
River volume (w.&d.)	No effect	This variable was combined with 'Section location in river' in the analysis	No
No. sediment patches	No effect	Strong effect on occurrence	No
Area of sediment patches	Mild positive effect on occurrence ($P<0.05$)	Strong effect on occurrence	Some
Presence of boulders & coarse debris	(Combined as 'Substrate') no effect	Strong effect on patch no.	No
Mean vegetation height	Negative effect on patch no. and abundance	Divided into 'tall' (negative effect on occurrence, patch no. and abundance) and 'short' (positive effect on occurrence, patch no. and abundance)	Yes

Vegetation type (species) >20% cover	Strong effect on abundance and occurrence measures	Vegetation type was not used as a variable, instead it was used to calculate Ellenberg scores	Yes
Ellenberg R/N/L/W scores	Not measured	Strong effect of light-demanding species	Yes
Grime C/S/R radius	Not measured	Varying effect	Yes
No. trees	No effect	*combined with canopy cover*	No
% canopy cover	Strong negative effect on occurrence and abundance	Negative effect on occurrence, patch no. and abundance	Yes
Evidence of grazing	No evidence	Positive effect on abundance	No
Section location in river (upper reaches)	Not measured	Strong positive effect on abundance, negative effect on occurrence and patch no.	n/a
Section location in river (lower reaches)	Not measured	Strong effect on occurrence and patch no. Negative effect on abundance	n/a

Table 2.3 Comparison between observed effect of environmental variables on Erythranthe guttata *abundance and occurrence measures, vs. the findings of Truscott, et al. (2008a)*

As demonstrated by Table 2.3, around half of the variables used by Truscott, et al. (2008a) agreed with the same or similar variables used in my experiment. The key differences were that no evidence of grazing, no effect of river dimensions, no effect of substrate and no effect of sediment patch availability was found in my experiment. My experiment differed slightly to Truscott, et al.(2008a) in methodology (my experiment was a survey of six valleys, whereas the authors surveyed a single large catchment) and data analysis (The authors used the Grime radius and Ellenberg indicator values). A catchment-level experiment in a single valley in the future may address some of these issues

2.4.1 Effect of environmental variables on *E. guttata* abundance and presence

The purpose of the survey was to determine whether the observed differences in measures of *E. guttata* occurrence and performance were attributable to the biotic and abiotic factors selected for study, whether these were consistent across years, and whether evidence exists to suggest that *E. guttata* is expanding its range within Banks Peninsula. If it is extending its range, may *E. guttata* be considered invasive? I reasoned that if the differences in occurrence/abundance measures of *E. guttata* reflect key measured abiotic and biotic factors, this should be relatively consistent across years. In contrast, if the biotic and abiotic factors show no consistency between years, this would indicate that either there is a major unidentified factor influencing *E. guttata* occurrence and performance, or that the identified factors are too general and must be further narrowed down in future studies.

E. guttata was present in 8.3% of all sites surveyed, across both years. This compares to 6% in the United Kingdom (Dawson and Holland, 1999) using data from the 1997 River Habitat Survey (Raven, et al., 1997) and 18% in a survey of New Zealand braided rivers (Williams and

Wiser, 2004). 8.3% is within the expected range for the habitat type and usage; Truscott, et al. (2008b) attributed their very high (85%) in Aberdeenshire to the high rate of channelization and disturbance within the region. Rates comparable to theirs (coverage of up to 95% of available habitat, see figure 2.10) were found in many highly channelized areas within Orton-Bradley Park, and in the areas developed for agricultural use (such as Kaituna Valley) in the Banks Peninsula region (Kerr, unpublished data), which suggests the observed rate could be attributable to human-mediated land usage and hydrological regimes. The survey confirmed that while there is some consistency between years, especially for the key factor 'shade', and that *E. guttata* occurrence and performance is significantly correlated with several the factors selected for study, other additional factors to the ones I chose for this study may be influencing the distribution of *E. guttat*a on Banks Peninsula.

Figure 2.10 Illustration of dense growth encountered during the surveys.

Left- A dense growth of *Erythranthe guttata* inhabiting a drainage ditch in Orton-Bradley park. Coverage for this 25m section was approximately 95% of total area of the waterway, including banks and bed. Note, the edges have been mowed. **Right-** A section of river bank in Kaituna valley, the curtain of growth extends approximately half a metre into the stream. This growth continued for another 10m either side of the photograph.

The results from both survey years confirm the expected negative influence of light availability/shade intensity on all *E. guttata* performance measures (Table 2.1). That is, shade has a negative influence on all performance measures. The positive effect of available sediment patches within the riverbed on *E. guttata* occurrence that was expected from the work of Truscott, et al. (2008) was severely limited in this study. This might be due to higher flow hydrological regimes causing greater disturbance of sediment and lower exploitation of patches, however further work is needed to establish the causes behind the limited effect. Overall habitat type was significant across both years (Table 2.3), forest and developed grassland types were strongly associated with abundance metrics. Vegetation type was strongly associated with abundance and occurrence, of interest was the association of Barley grass (*Hordeum vulgare*) with *E. guttata*; 73% of sites with *E. guttata* populations were recorded as being accompanied by Barley grass.

2.4.2 Evidence for an ongoing invasion of the surveyed regions by *E. guttata*

The metric of range expansion to define invasions as detailed by Richardson, et al. (2000) (>100m over 50 years for seeding species, >6m over 3 years) is of value but should be regarded with some caution. Both the Orton-Bradley and Te Oka valley populations showed growth patterns that are consistent with Richardson, et al. (2000)'s metric of invasion. This result is not totally conclusive; however, the balance of evidence tends to support the hypothesis that populations are expanding their range within the region and are most likely to be invasive.

2.5 Summary

The biotic and abiotic environmental variables in this study influencing *E. guttata* abundance and occurrence appear to be mainly those associated with light availability, local plant community structure and local habitat characteristics. Shading intensity has a strong negative association with *E. guttata* occurrence and abundance. Vegetation type, the presence of Barley grass (*Hordeum vulgare*) is also strongly associated with these metrics. I therefore hypothesise that *Hordeum vulgare* may have an interactive relationship with *E. guttata* that influences plant performance and explains this trend.

In general, measures of abundance and occurrence agreed in terms of biotic and abiotic factors influencing their measurements. This is promising as it suggests that occurrence in this case may be a useful metric for rapidly assessing impact of invasions elsewhere, however more research is required to substantially demonstrate this. Further research is required to clarify the relative importance of these and other abiotic/biotic factors and identify whether as-yet unexamined factors can better explain distribution trends. The influence of river characteristics (sediment patches, hydrological regime, substrate and local biota) deserves more in-depth study; the evidence suggests additional factors are at play in determining distribution. Additionally, the difference of this result to that of Truscott, et al. (2008a) suggests that further research, possibly a more granular approach to smaller regions, may be worthwhile in the future.

The populations surveyed fully over both years (Orton-Bradley and Te Oka) show relative upward expansion over the period (fig 2.6). This result must be weighed with the fact that

identified populations do exist in higher tributaries above the surveyed zone, so inputs of fragmentary propagules and/or seeds from these may establish downstream. This raises the question of whether the population is indeed expanding, or whether inputs of propagules from upstream are establishing in available habitat with relatively few fragmentary propagules establishing upwards from the downstream population. More research is needed to answer this and other questions around the reproductive strategy of *E. guttata* in the region.

Chapter 3

3. Testing for a persistent seed bank

3.1 Introduction

Invasive plants are a serious threat facing riparian ecosystems, home to many endangered and threatened species. *Erythranthe guttata* is a clonally reproducing weed with potential to spread very rapidly through riparian systems by forming a network of ramets surrounded by dense mats of stolons that rapidly colonise the surrounding area (Matthews, et al., 2012). Of concern is the rapidity which this weed can colonise after disturbance (Matthews, et al., 2012). Soil seed banks are a part of biogeography that concerns the dispersal of seed that remains dormant but viable, often for many years. They play a major role in species succession, particularly in disturbed or manmade environments (Goodson, et al., 2001). Many weed species form seed banks, and they are a significant source of invasive population; Kropac, (1966) estimated the potential weed population from seed banks in agricultural regions to be 39.8-140.6 million individuals per hectare (Kropac, 1966).

E. guttata seeds are known to persist in the soil between growth seasons (overwintering) (Elderd and Doak, 2006) and their presence in the germinable seed bank has been noted previously in other countries (Truscott, et al., 2006) and has been detected in seed banks without any living specimens present, indicating that long-term survival is possible (Goodson, et al., 2002)

A common reproductive strategy of clonal invasive plants is exploitation of openings in otherwise inhospitable areas such as light gaps in canopies using small, numerous seed that persist in the environment (Kanno and Seiwa, 2004; Wang, et al., 2013; Hara, et al., 2004; Matlaga and Horvitz, 2009). This trait permits opportunistic expansion into disturbed areas before native cover that would otherwise crowd out the invasives can fully recover. It is of particualar value when control techniques remove biomass but do not prevent regrowth (ie. mechanical clearance) (Kanno and Seiwa, 2004) .Description of seed bank dynamics and invasive plant species seed persistence within the seed bank is important to invasion biology and conservation, as it illuminates the potential regrowth characteristics of an invader and how long the source of propagules will continue in the absence of further introductions (Gioria and Pysek, 2015). Understanding seed bank dynamics may also inform potential methods of preventing invasions through manipulating seed bank content (Guido, et al., 2017)

3.1.1 Relevance to Banks Peninsula

Banks Peninsula currently retains a mere one percent of its former forest cover and is home to many flora and fauna species unique to the area (Wilson, 1992). The region is an important habitat for other native New Zealand species, particularly those inhabiting riparian zones. (Environment Canterbury, 2018). Truscott, et al. (2008b) identified a significant negative association between *E. guttata* coverage and local plant species diversity, and a major effect of *E. guttata* on the structure of riparian plant communities (Truscott, et al., 2008b). Understanding the local seed bank dynamics and content is valuable to conservation efforts, particularly in the context of developing whole-system approaches to land management and predicting impacts on native species (Gioria and Pysek, 2015). Additionally, changes in the

local seed bank composition through invasion have been shown to have negative effects on biodiversity (Fisher, et al., 2009).

This experiment is of value to my research as it will provide context to the results of Chapter 2. As previously identified, soil seed banks are a critical factor in landscape-level persistence; hence an investiagtion of whether a soil seed bank is present in the location studied will help reveal the reproductive strategy of local *E. guttata* populations. Seed banks, seed germination and seed survival themselves are influenced by local environmental biotic and abiotic factors (Mahmood, et al., 2016; Joet, et al., 2016; Humphries, et al., 2018). Differences in local environment between valley locations may cause differences in local seed bank dynamics. As such, seed bank dynamics can be considered a conglomerate biotic factor, itself a product of other environmental factors (Mahmood, et al., 2016; Humphries, et al., 2018) influencing plant species abundance and occurrence in general (Savadogo, et al., 2017) as well as weeds like *E. guttata*.

3.1.3 Objective two

The first objective of this chapter is to determine whether valley locations with identified *E. guttata* populations have a persistent seed bank. The aims of this objective are to quantify the overwinter survival rate of seed, combined with known germination rates to calculate the potential yearly growing season seedling population. The second objective of this chapter is to determine whether differences exist between locations, and across different sampling times, particularly immediately prior to, and after the flowering season.

3.2 Methods

3.2.1 Experimental background

Distribution of seeds in soil is often highly clustered according to dispersal characteristics and suffers from the issue of high spatial variance in seed density. Bigwood and Inouye (1988) conclude that many the smallest sample size practical is advantageous over a smaller number of larger samples due to this effect (Bigwood and Inouye, 1988). Formulae have been proposed to calculate the necessary number of samples and their volume (i.e. Champness (1949) and Rabotnov , (1958)) however these have been shown to have potential reliability issues in the field (Bigwood and Inouye, 1988). Warr, et al., (1993) suggests a sufficient number of samples is +50, adding that a large number of previous studies using fewer than 40 samples are unreliable (Warr, et al., 1993). Timing of sampling is important to accurately identifying seed bank dynamics; the seeds in transient seed banks which germinate during autumn will be absent during winter and spring. Those which remain dormant during winter and germinate during spring are best identified during early-mid spring (Warr, et al., 1993). My sampling design therefore aims to capture this dynamic in the October sampling, as well as the total germinable seed bank in the post-flowering (late summer) period. Estimation of total seed numbers in soil samples can be achieved quite simply through concentrating seeds in the sample by washing or flotation and counting the extracted seed, however variable seed viability confounds this method when used alone. Combination of this method with germination study has been shown to have excellent results, a modified method of which is used here (Ter Heerdt, et al., 1996) Tetrazonium viability tests were considered, however Warr et al. (1990) notes that this test using small seed sizes (such as those of *E. guttata*) is technically difficult to achieve. More complex methods of such as cold-stratification or elutiration have better results

with lower sample numbers (Gross, 1990) however these tend to be resource and time-intensive.

3.2.2 Choice of populations

Three valleys were chosen from the original six (Chapter 2) to be used in the study of persistent seed banks. The three chosen were; Kaituna Valley, Te Oka Bay and Orton-Bradley Park. Each valley has confirmed populations of *E. guttata* and represent three distinct habitat types; (1) lowland, flat farmland with patches of dense bush in open fields, (2) tussock undeveloped grassland and regenerated native bush and (3) developed grassland, non-native forest with native bush in upper reaches. Where abbreviated, they will be referred to in this section as 'KAI', 'TOK' and 'OB' respectively.

3.4.3 Sample collection

A preliminary study of seed germination rate in 8 of 10 petri dishes (two dishes developed fungal infection prior to germination and were discarded) of 100 seeds each collected in summer 2017/18 established a flowering period greenhouse germination rate of ~70%, +/- ~10%. (Kerr, unpublished data)

From the three valleys with identified *E. guttata* populations, 17 sections were identified as having recorded open sediment patches. 79 sediment samples (22 from OB, 24 from KAI & 33 from TOK) were collected using a random allocation method; each site was located using its GPS tag, then a patch was randomly selected from those available within the 50m limit. Sediment was collected using a trowel to a depth of 2.5cm in a 20x20cm quadrat placed on sediment patches to collect a 1L sample. Samples were returned to a greenhouse at the University of Canterbury, where large stones, vegetative material and other solid detritus was removed. Removal of all soil to concentrate the samples was found to be impossible due to the

relatively similar size of *E. guttata* seeds to the grain size of the soil. Samples were placed out in labelled aluminium foil trays and observed daily for 7 days. The sediment samples were kept moist during this period using a watering can and later with the installed greenhouse misting system. Daily greenhouse temperature ranged between approximately 17 and 28ºC. Excess water was drained, and trays perforated to provide drainage. The trays were photographed daily during the observation period to record seedling appearance. After the 7-day observation period, the trays were periodically observed for another 3 weeks, at the end of which seedlings were identified and counted. The experiment was conducted in two parts (Pre-flowering and post-flowering). The pre-flowering portion took place from the 9th of October 2018 and was concluded on the 6th of November. The post flowering portion took place from the 17th of April to the 22nd of May

3.4.4 Data Analysis

An ANOVA was used to calculate the effect of location and collection time on germination rate. A significant ANOVA result for collection time would indicate there is variation in the standing seed bank, irrespective of location and indicating consistent seed survival across the tree locations. A significant result for location would indicate there is variability in seed survival rates, but there is limited input/output from the seed bank (i.e. Few seeds germinate & few survive to germinate). This would suggest a limited role of the seed bank in population spread; either most of the set seed fails to germinate due to an environmental factor, or seed germinates rapidly upon dispersal and does not contribute to the standing seed bank. If the interaction between location and collection time is significant, it implies there is variation among the location with respect to seed bank characteristics. The null hypothesis of the ANOVA is that there is no significant difference between seedling counts. The temporal

dynamics of any seed bank are identified by comparing the early spring germination rate with late summer. If a low spring/high summer rate is observed, this would indicate that most seed germinates in late summer/autumn and does not overwinter. A high spring/low summer result would indicate that most seed germinates in spring, and dormancy prevents germination of the set seed over winter. A non-significant result between sampling periods may indicate that an un-observed process (such as spatial heterogeneity or local adaptation) is confounding the results.

3.5 Results

Analysis of variance (Table 3.1) showed that location and collection time were both significant when comparing between sampling periods. Location was also significant among sampling periods.

Variable	Between sampling periods	Among sampling periods
Location	***	***
Collection time	***	
Interaction	ns	

Table 3.1 ANOVA Results of between and among sampling period Erythranthe guttata *seedling count data. Ns; non-significant, *; P<0.05, **; P<0.01, ***; P<0.001.*

Mean seedling count (table 3.2) showed that Orton-Bradley park had consistently higher seed germination than the other two locations, across both periods. Te Oka showed the greatest change in seedling count (27x)) followed by Orton-Bradley (21.811x). Kaituna showed the lowest change (5.2x) and the lowest mean seedling counts/L.

Location	Mean seedling count/L (Pre-flowering).	Mean seedling count/L (Post-flowering)	Mean difference pre-post flowering (x)
Orton-Bradley Park	1.591	34.7 $^{3\ s.f.}$	21.811
Kaituna Valley	0.125	0.650	5.2 $^{3s.f.}$
Te Oka Bay	0.333	9.0 $^{3\ s.f.}$	27.0 $^{3\ s.f.}$

Table 3.2 Erythranthe guttata *seedling count data per Litre of soil, by valley location and collection time (Standard deviation in brackets)*

3.6 Discussion

From previous work with similar species, we know that the reproductive strategy of *E. guttata* may be a two-pronged sexual/clonal effort. The output of clonal growth is considerable and is a powerful means of spreading rapidly along waterways. The role of sexual reproduction and seed set in *E. guttata* range expansion and local persistence has had relatively little academic attention in comparison to other invasive species such as *Hydrangea paniculata* (Kanno and Seiwa, 2004) and *Iris japonica* (Wang, et al., 2013) to name a few.

This greenhouse experiment confirms that the *E. guttata* populations within the region do produce a germinable, overwintering seed bank. This implies that there is at least a useful role for set seed; i.e. the pressures that might cause an overwintering seed bank to be absent- seed abortion, lack of fecundity, predation and soil micro-flora, are insufficient to prevent a seed bank forming. However, given the potential seed set of *E. guttata* (At observed rates of stem density and seed set, 25,000 seeds per m2. Kerr, Unpublished data) the observed germination rates seem low. Truscott, et al. (2006) observed a 33% germination rate within 9 days, which may explain the low rate of germination in sampled seeds, however experiments in California establish the yearly overwintering seed survival rate at 53.4% (Elderd and Doak, 2006). Further research is required to establish how the overwinter survival rate in New Zealand soils, seed fertility rates, pollination dynamics and other aspects of sexual reproduction influence total seedling population.

Collection time showed a significant difference in germination rate; between the pre-flowering collection and post-flowering collection. The post-flowering collection had significantly greater mean seedling counts (49 in pre-flowering vs. 887 in post flowering), which was consistent across valley locations. This indicates that much of the set seed may germinate shortly after flowering; whether this is primarily the result of environmental conditions or temporal biochemical cues may be of interest for future studies in this field.

Orton-Bradley Park showed a considerably greater seedling count than the other sites, consistent across sampling times. However, the difference in seedling count between collection times was comparable to Kaituna Valley, even though the latter had a much lower overall seedling count in both the (1.591/46.247 vs 0.333/18.590 respectively). The results of samples from Kaituna Valley and Te Oka were also contrary to expectations; I expected a much greater rate of seed germination from Kaituna Valley than was observed, and indeed Te Oka showed a somewhat higher rate that Kaituna Valley. This expectation was based on the much larger *E. guttata* population observed in Kaituna Valley in comparison to Te Oka.

The result of this experiment strongly suggests that one or a combination of factors (heterogeneity of seed deposition, valley-level variance or local adaptation) may be responsible. Of these, heterogeneity is the most likely candidate, as distribution of both seeding plants and seed banks may be strongly influenced by environment (Truscott, et al., 2006; Warr, et al., 1993). Differences between valley locations, such as nutrient inputs, local soil mineral content, micro climate etc. may have significant impacts on seed deposition as well as seed survival. Further studies of germination rates of collected seed may highlight whether the

observed trend can be attributed to local environment, or whether functional differences exist in seed characteristics (overall seed set, viability, abortion rate etc.) exist between locations.

3.7 Summary

Using the above experiments, this experiment identified a persistent *E. guttata* soil seed bank in the Banks Peninsula region. Additionally, a portion of the temporal dynamics of set seed were investigated, and a disparity between collection times was also identified.

The observed variation in seedling counts between sampling periods, and between locations indicates that seed bank dynamics within the region may not be a simple affair of seeds waiting for the right time to germinate. It suggests that complex local environmental factors, as well as internal biochemical or genetic ones may be affecting the behaviour of seed in the environment and thus the soil seed bank dynamics of *E. guttata* in the region.

Chapter 4

4. Relative impact of shade & competition on *E. guttata* performance metrics

4.1 Introduction

4.1.1 Background

As ecosystems are increasingly stressed by human activities, pollution and climate change, potential threats to native biota need to be closely examined to economise finite conservation resources and direct effort where it is needed most. Invasive plant species have come under

intense scrutiny to understand the drivers behind their performance in novel environments. (Wadsworth, et al., 2000; Alpert, et al., 2000; Drake, 1989) The complex genetic, physiological and environmental factors behind invasion success are yet to be fully understood in general, and many species still require further work to understand how they interact with the environment.

Erythranthe guttata is absent from biosecurity evaluations (Ministry for Primary Industries, 2019) , however it may pose a significant threat to the economy and native flora of New Zealand. It shows many characteristics of successful invaders; rapidly growth in dense patches that can completely smother large patches of riverbank (Grant, 1924) prolific dispersal (Truscott, et al., 2006), rapid germination (Elderd and Doak, 2006) and potential to establish persistent seed banks (Elderd and Doak, 2006).

Various hypotheses exist to account for the temporal and spatial dynamics of invaders (Pysek and Hulme, 2005, Bradley, et al., 2011, Heger and Trepl, 2003), these focus primarily on the invasive species themselves, and analyses of the effect of host environments are often limited to range expansion within man-made or degraded habitats. Assessing dynamics of range expansion on a granular scale within a geographic zone provides context to studies with broader scope, which may be of limited value when considering widely varying environments. Experiments that study performance under stressors have potential to provide detail about pressures, physiological trends and trade-offs in function and form that may not be evident under normal conditions (Pigliucci, 2005). The experiments in this chapter aim to assess how

populations respond to real-world environmental variables and draw conclusions in combination with known *E. guttata* properties.

Highly disturbed habitats show greater vulnerability to invasion by alien plants, as previous competitive barriers (light, nutrient availability, toxic defences etc.) are temporarily disrupted, allowing the invader to establish (Lozon and MacIsaac, 1997; Hobbs and Huenneke, 1992; Kneitel and Perrault, 2006). Subsequent disturbances post-introduction allows further infiltrations, progressing the invasion. The hydrology and geography of Banks Peninsula in particular (fast flowing rivers, deep valleys and frequent disturbance by storms, livestock and human activity) mean that the area is well suited to invasions

4.2.2 Interaction of shading and competition

Light availability has been strongly connected to the performance and ecology of *E. guttata* (Truscott, et al. 2008a, Collins, et al., 2018) and other invasive species (Kanno and Seiwa, 2004; Alpert, et al., 2000; Matlaga and Horvitz, 2009). Light dependence is a key distinguishing character of plant species, as described by Ellenberg (1988) in his indicator values which include light dependence/shade tolerance. Species to species interactions can be facilitative or competitive and typically shift from positive (facilitative) to negative (competitive) along productivity gradients (Holmgren, et al., 1997). Heterogeneity in competition intensity means invasive species typically show spatial patchiness in the initial stages of invasion, but the dispersal characteristics of alien plants such as wind or animals allow transport past minor barriers for colonisation beyond these limitations. (Bradley, et al., 2011; Alpert, et al., 2000; Vickery, et al., 1986). Generally, plant interactions are proximity

dependant and reach equilibrium between environmental disturbances (Holmgren, et al., 1997).

The combined effect of neighbour species and shading is less well studied than the individual effects: work by Elderd (2003) investigated the effect of grass thatch (dead plant material) accumulation and shading on *E. guttata* reproductive and physiological performance. In his study, Elderd (2003) linked thatch accumulation with decreased seed germination, plant height and increased insect herbivory. Additionally, he identified a shading threshold effect where plants grown under high shading and grass thatching experienced much lower rates of seed germination. Finally, plants under thatching treatment displayed higher rates of side stolon growth. However, this evidence is opposed by the results of Truscott, et al. (2008a), who found that light availability, as well as interspecific competition were key predictors of *E. guttata* occurrence and abundance metrics. They found areas with ruderal and stress-tolerant neighbour species to be more commonly colonised than taller vegetation. This raises the question of whether the presence of *E. guttata* in areas with high light availability and ruderal and stress tolerant vegetation is a result of *E. guttata* sharing similar ecological niche parameters with ruderal species or an interactive facilitative relationship.

4.2.3 Effect on plant performance metrics

When exposed to stress, plant performance is altered in response. Plasticity allows stoloniferous plants to respond to variations in resource availability by intensifying growth in patches of more favourable habitat. This behaviour, called ‘Foraging’, is not limited to clonal plants and describes the ability of plants to project leaves and roots outward to seek resources

in their locality (Grime, et al., 1991). Typical forms of clonal growth fall on a scale between tight clumps of ramets, to broadly spread groups connected by narrow stems. The exact response pattern tends to vary between horizontal and vertical outgrowth; different species and levels of plasticity as well as environmental factors are a primary factor behind this (Weijschede, et al., 2008; de Kroons & Hutchings, 1995). The role of projected ramets in stoloniferous plants is clonal integration; Clonal integration allows translocation of resources such as carbohydrates, water and minerals between interconnected ramets, increasing patch viability and reducing the impact of spatial heterogeneity of resources (Wang, et al., 2017).

4.2.4 Measurements

Measurement of physiological variations expressed can be useful as a simple metric of otherwise complex underlying stressors (Hashimoto and Nonami, 1990). Morphology of stoloniferous plants is relatively simple to quantify with a few parameters; longest internode length and longest leaf measurements are valuable tools for measuring physiological performance: Longest leaf measurement is a commonly-used metric of plant size (Wesselingh, et al., 1997). Internode length can be used as measure of 'Foraging', where the plant spreads ramets to avoid stressors or vacate low quality patches, (Huber, et al., 1998; Hutchings & de Kroon, 1994). Greater internode length and hence increased foraging can mean the environment is heterogeneous and the plant is exploiting local areas of high resource availability (Birch and Hutchings, 1994) however it can also be an indicator of resource stress as a result of competition (Weijschede, et al., 2008) or shading (Hutchings and de Kroon, 1994)

4.2.5 Summary & objectives

The objective of this chapter is to determine whether evidence exists to indicate interspecific competition from Barley grass (*Hordeum vulgare*), affects *E. guttata* performance, and to draw conclusions on whether the observed neighbour species trends in Chapter 2 the result of shared niches or interactive relationships may be and to determine what form (competitive, neutral, facilitative) any observed interspecific relationship takes.

4.3 Methods

4.3.1 Experimental background

Greenhouse experiments are a standard method of testing whether differences observed in the field are the result of a factor, without potential confounding effects of the local environment. As well as being a controllable environment, they also remove potential confounding factors of varying habitats as well as the impact of the invasive species itself, which may have caused significant irreversible ecosystem damage (Zaveleta, et al., 2001).

4.3.2 Experimental design

A common method of investigating the relative impact of two factors on plant performance is the use of the Latin Square experimental design. In this experiment, two shade intensity treatments (50% and 70%) were tested against a control and one competition treatment (addition of a grass neighbour species) in two experiments (Table 1).

Experiment 1			Experiment 2		
	0% shade	**50% Shade**		**0% Shade**	**70% Shade**
No Competition	Control	50%/No Seed	**No Competition**	Control	70%/No Seed
Competition	0%/Seed	50%/Seed	**Competition**	0%/Seed	70%/Seed

Table 4.1 Experimental design of shading/competition Latin square experiment

4.3.3 Materials and methods

I conducted the two experiments in this chapter in a glasshouse at the University of Canterbury, Christchurch. Source material was taken from a large clonal growth in Orton-Bradley Park (OB). Using internode cuttings, a standing population of 25 plants were grown under a constant watering and temperature (22 degrees Celsius) regime in a greenhouse over 3 months. 10 plants were used to provide leaf/stem/root cuttings for the first experiment and a further 8 were used in the second. I took cuttings from a random sample of a stock of healthy plants grown in a greenhouse from tissue samples of single plants taken from Orton-Bradley Park. Cuttings included a minimum of 5cm of stem, roots and two developed leaves to simulate an 'ideal' fragment: In preliminary experiments, internode cuttings had ~60% greenhouse survival rate, whereas stem, root and leaf cuttings had ~95% rate (Kerr, unpublished data). This was attributed to internode cuttings having lower leaf and root mass to stem mass ratio, which reduced their ability to survive cutting and transplant shock. I planted the cuttings in 11x11cm pots with potting mix and a slow-release fertilizer, then placed in a misting cabinet for 7 days before being placed out into trays with ~15cm spacing between each pot.

The observed mean growth rate of *E. guttata* in greenhouse conditions (400lux, 22 degrees Celcius, water *ad libertum*) was ~15mm/wk (longest leaf length) and ~10mm/wk (longest

internode length) (Kerr, unpublished data) . From this I determined that an experimental duration of 5 weeks would allow any effect of shading or competition to appear while excluding the potential confounding factor of plants interfering with each other's growth.

Each treatment was assigned to 40 pots, which were then set up two tables, one with a shade cloth supported by a frame and one without. I assigned each pot a non-repeating random number within their shade category and assigned a position according to numerical order to control for spatial variation in greenhouse conditions. Pots were then set out in 16, 10cm deep trays evenly spaced on two tables with 5 pots per tray. Each tray had a water line installed, which was set up to maintain a constant water level in the trays and was checked regularly.

Control treatment (No competition/No Shade):

Plants grown in full light (~1000lux), with no neighbour species seed added.

Competition treatment:

Plants grown in the same light intensity as the control, with 10 neighbour species seeds spread evenly per pot, pressed 1cm into the surface. The competitor species selected was a commercial cultivar of Barley grass (*Hordeum vulgare*).

Shade treatment

Plants grown under two thicknesses of shade cloth in partial shading; ~500lux (50% shade) and ~300lux (70% shade) compared to a midday sun intensity of ~1000lux. A large metal frame was set up on two tables to support shade cloth of two grades; 50% and 20%. For the 50% shade treatment a single layer of 50% grade cloth was used. For the 70% treatment a layer of each grade was used. Shade cloth was pegged in place to prevent light patches and allow access for measurements and maintenance.

Data loggers (HOBO Pendant ® Temperature/Light 64K) collected temperature and light readings in each shade intensity treatment at 10-minute intervals throughout the run of each experiment. Temperature/light data processing was completed using HOBOware Pro (Onset Computer Corporation)

4.3.3 Physiological measurements of plant growth

Plant performance measurements I used for this experiment were:

- Mean longest leaf (middle value of the two longest leaves on each plant)

  Longest leaf length is a commonly used measurement of relative plant size (Wesselingh, et al., 1997; Lockard, et al., 1985) and provides a metric of investment in overall growth.

- Longest internode length.

Longest internode length is a measure of stress avoidance (de Kroon, et al., 1998; Weijschede, et al., 2008)

I measured leaves with a set of verniers from the leaf tip to the basal serration (see fig 3.)

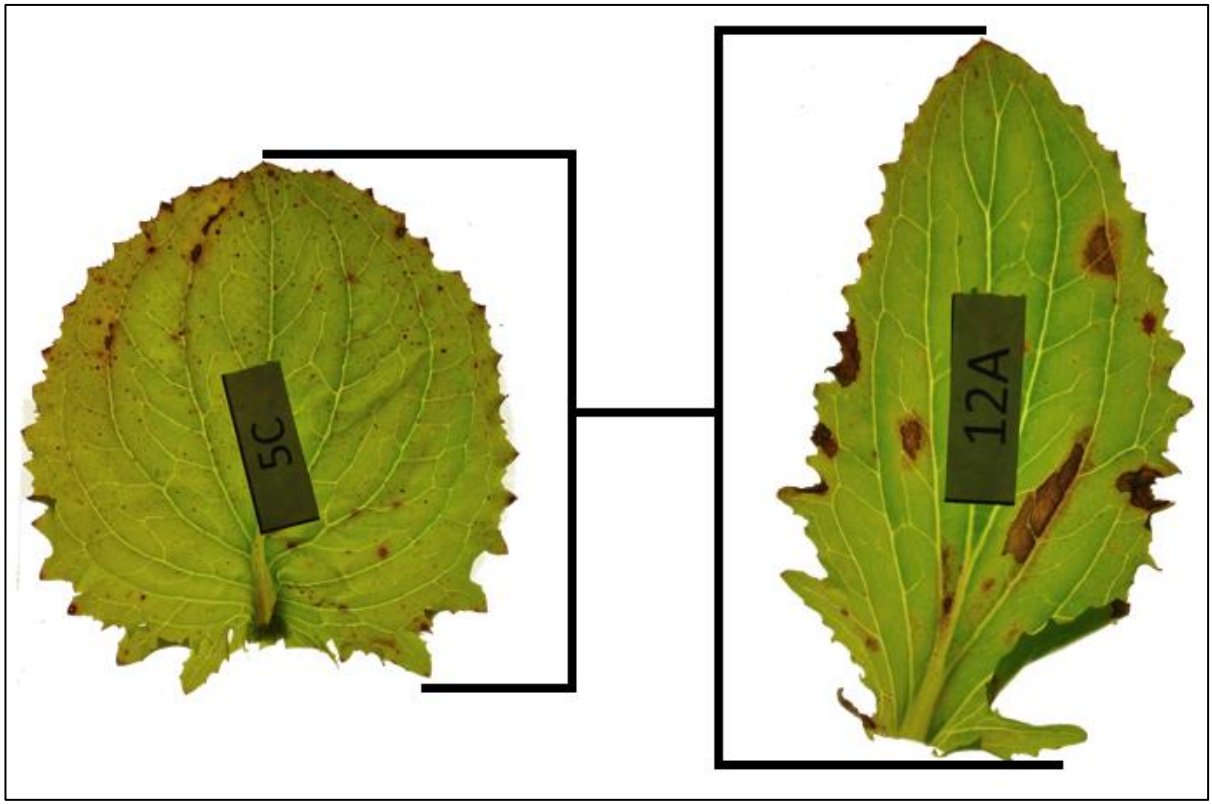

Figure 4.1. Longest leaf (Basal serration to leaf tip) measurement- (Photo Michelle Williamson, 2018)

I measured internodes from the base of each internode to the other, with the stem straightened out to remove any effect of bending. I selected the longest internode selected visually, and then confirmed using the verniers.

4.3.4 Analysis

Tests for differences in performance metrics between treatments were done using pairwise ANOVA. The two factors were shade and competition, with their interaction as a separate factor. The shade factor represents the shade treatments with levels 0%, 50% and 70%. The competition factor represents the seed treatments, with two levels; no seed added, and 10 seeds/pot added.

The purpose of the greenhouse shading/competition experiment was to determine whether the differences observed in chapter 2 in *E. guttata* occurrence and abundance between 50m sections with the ubiquitous agricultural grass species (*Hordeum vulgare*) and other species is a result of neighbour species interaction. If this variation is a result of a competitive or facilitative effect, the greenhouse plants should exhibit differences in performance between those with and without neighbour plant species. If performance measures show no significant variation between the competition treatments, it suggests the variation identified in the field is likely a result of heterogeneity in the environment.

4.4 Results

Analysis of variance was conducted on each performance metric to investigate if any significant differences were present among shade and competition treatments. A significant result for shade treatment would indicate a performance differential between shading intensities across the two competition treatments. A significant result for competition treatment would indicate a performance differential between competition treatments across shading intensities. A significant result for both would indicate a synergistic or antagonistic effect between shading and competition treatments on performance metrics.

Each performance metric measures a different effect of each treatment. A significant result for longest leaf measurement for either treatment would indicate a performance deficit, resulting in lower whole-plant mass. A significant result for longest internode length for either treatment

would indicate that there is significant 'foraging' to avoid resource stress and seek areas of higher resource availability

The ANOVA results indicate no significant difference between competition treatments (Table 2) for either performance metric. The shading treatment showed a significant difference for both metrics. Interaction between competition and shading was non-significant for both metrics.

	Competition		**No competition**		
Performance measure	50% shade	70% shade	50% shade	70% shade	Control (0%)
Longest Leaf	ns	***	ns	***	ns
Internode Length	ns	**	*	*	ns
Interaction	Ns				

Table 5 Analysis of variance for differences in performance metrics among shading treatments, competition treatments and among groups (competition: shading).

Multiple pairwise comparisons of the treatment means using Tukey's HSD test were performed to determine which treatment means differ significantly from each other (95% confidence interval, H_o: difference=0).

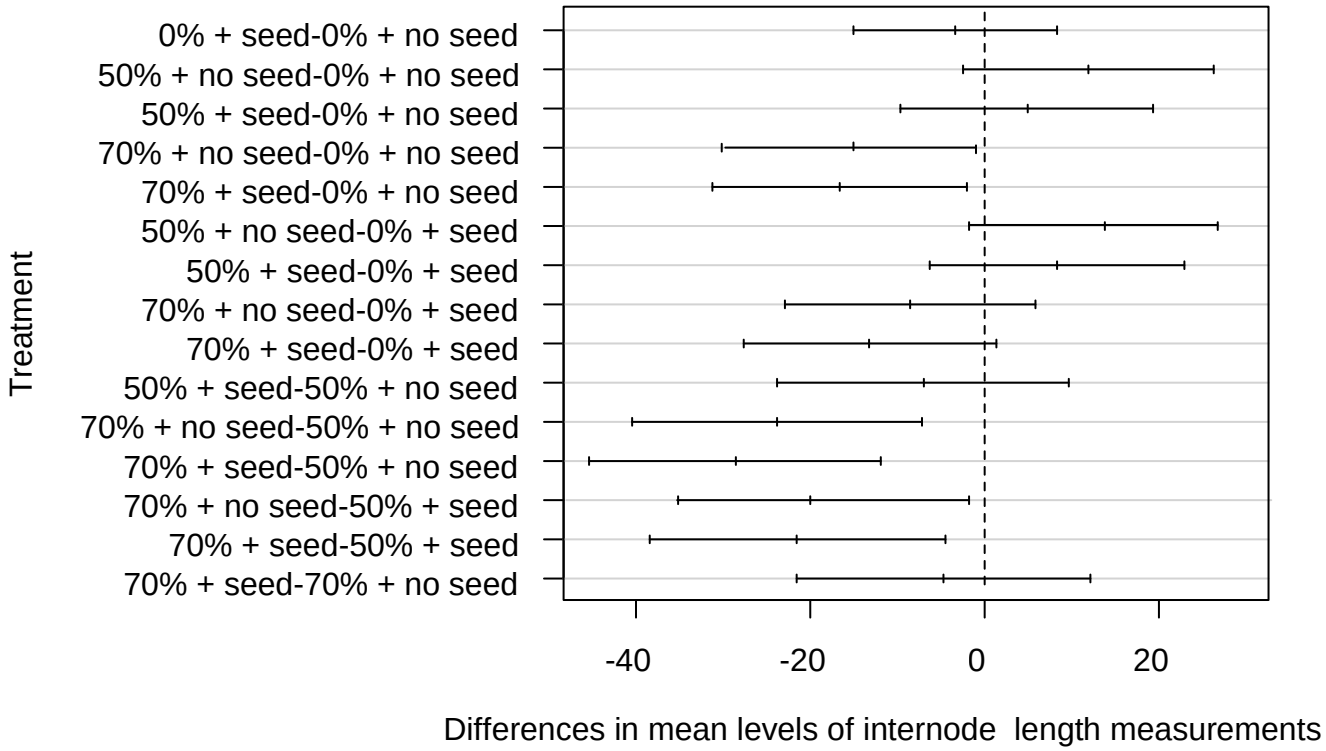

Figure 5.1 95% confidence interval plot for different levels of shade/competition treatment, for internode length. 'Seed' refers to level of competition treatment. 'No Seed' means no Barley seed was added.

The effect of shading and competition on internode length measurements are shown above in Figure 5.1. Critically, comparison of different shading intensities (i.e. 70% and 50%) across all possible combinations of competition showed no difference. All comparisons of identical shading intensities with different competition treatments were non-significant.

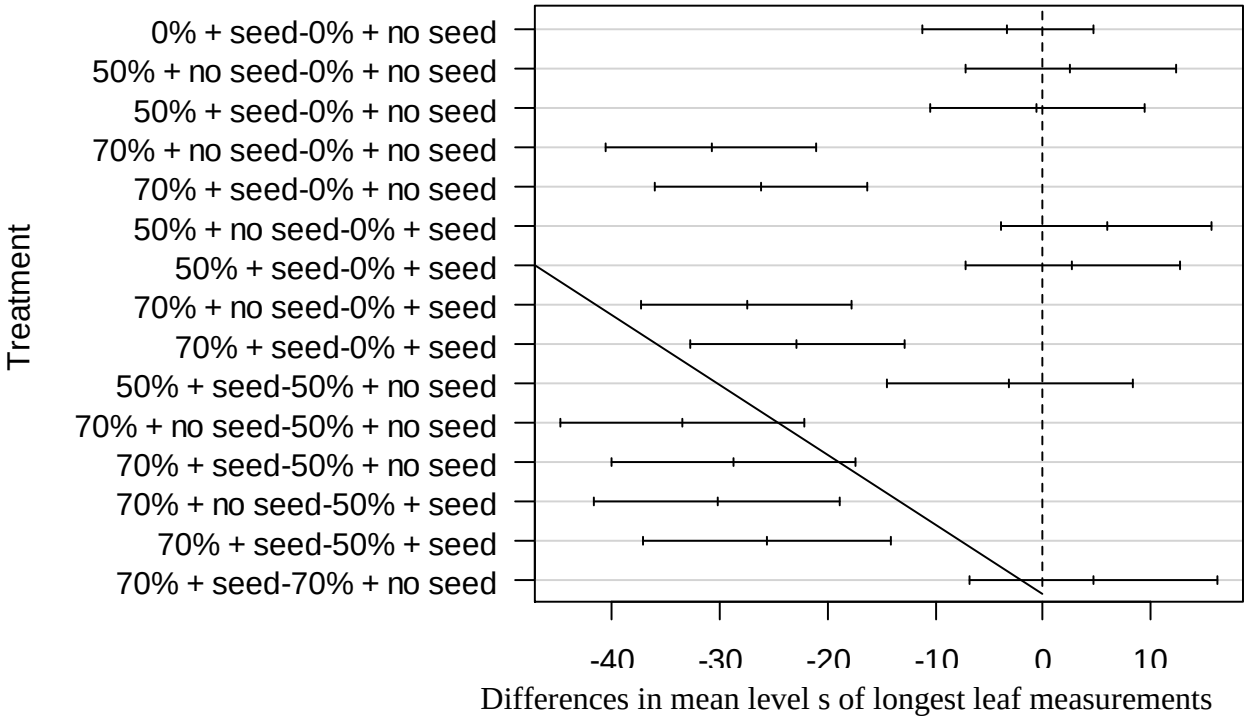

Figure 5.2 95% confidence interval plot for different levels of treatment, for longest leaf measurements

The effect of shading and competition on longest leaf measurements are shown above in figure 5.2. As in the previous figure, when different shading intensities are compared, there is no significant difference between all combinations of competition treatments. Additionally, all comparisons of identical shading intensities with different competition treatments were non-significant.

4.5 Discussion

From previous work on the effect of shading on *E. guttata* (Elderd, 2003; Collins, et al., 2018 and Truscott, et al., 2008a) and other light-dependant clonal species (Kanno and Seiwa, 2004) (Matlaga and Horvitz, 2009), we know that shading is a key limitation on *E. guttata* growth. Additionally, interspecific competition has been suggested having an influence on patch size and stem number (Truscott, et al., 2008a). The effect of an environment's species richness is a

well-established concept in invasion biology, however there are often considerable location-dependant caveats to this rule (i.e. Hood and Naiman, 2000; Levine and D'Antonio, 2003; Richardson and Pysek, 2006). Importantly, Daehler (2003) found in a meta-analysis based on 79 case studies that native-invader competition dynamics are largely context-dependant and rely heavily on the environmental conditions and characteristics of the species concerned (Daehler, 2003).

For this greenhouse experiment, populations were sampled from a single site within the Banks Peninsula area and cuttings grown into adult plants which were then used as source material for the experiment. The objective of this experiment was to determine whether the observed association of population stem density and patch size with *Hordeum vulgare* presence in the field may be attributed wholly or in part to neighbour species interaction, or whether the variation may be more the result of shared environmental niches.

No effect of competition on either performance metric was found. Although shading did influence these metrics, there appeared to be no synergistic effect of competition and shading. Critically, this means any explanation of why *E. guttata* appears to be associated with *Hordeum vulgare* should look at environmental factors shared with neighbour plants. Therefore, the relationship between these two species may be considered 'neutral' in respect to the two metrics used in this experiment.

4.6 Summary

E. guttata performance deficits under shading conditions have been identified in several studies (Elderd, 2003; Truscott, et al., 2008a; Truscott, 2007). Two measures of performance showed no significant difference between competition treatments. This suggests that any interaction between *Hordeum vulgare* and *E. guttata* is unlikely to have caused the observed variation. This contradicts the initial expectations; as discussed earlier there is significant evidence for neighbour species affecting *E. guttata* performance specifically and invasive plants in general. However the majority of the literature looks at the body of competitor species as a whole, or other environmental effects (such as accumulation of dead matter occluding light, relative height & Ellenberg Indicator values) (Truscott, et al., 2008a; Elderd, 2003), rather than the functional effect of a single species. The object of this approach is to separate a single species at from the local biota and examine its effect on an invasive weed. This approach has value as it is often difficult to pin down models of species interactions to cause-and-effect relationships (Connell, 1990; Pigliucci, 2005) and this result compliments other research into species-species interactions with *E. guttata*, i.e. Elderd, (2003).

The decision to use single-source clonal plants rather than include plants from all three locations where *E. guttata* was found (to control for variation between locations) was taken based on logistical limitations of greenhouse space available at the time. Future research could aim to identify whether local adaptation influences performance measures between valleys.

Chapter 5

5. General discussion and conclusion

5.1 Factors influencing *E. guttata* distribution and density

Several biotic and abiotic factors influence metrics of *E. guttata* distribution and density (Truscott, et al., 2008a). In Chapter 2, two surveys were undertaken to determine what factors previously identified by Truscott, et al. (2008a) have a significant effect on *E. guttata* distribution and density within the Banks Peninsula region. For this experiment, six geographically separate valley locations were selected within the region and site data, including biotic and abiotic variables and *E. guttata* population abundance metrics, was collected. To assess the whether the populations were static or dynamic, the second survey was conducted at a year's interval. The site variables measured in each 50m section were:

- shading intensity (canopy coverage)
- substrate type
- habitat type
- river dimensions (water depth & width)
- number of trees
- height of vegetation
- primary vegetation type
- total area of sediment patches

The *E. guttata* metrics sampled were:

- stem density

- patch area
- number of patches
- whether evidence of herbivory was apparent

The site variables were a subset of a group previously identified by Truscott, et al. (2008a) as being associated with *E. guttata* population metrics in a study in rural Scotland. If these traits are also associated with *E. guttata* population metrics in New Zealand, then the findings of this study and those of Truscott, et al. (2008a) may be of value in characterising the vulnerability of environments to invasion by *E. guttata*. However, if the results differ substantially from those in Scotland, this will suggest that New Zealand populations respond differently to environmental conditions than those in Great Britain.

Some of the site variables chosen showed association with *E. guttata* abundance and occurrence (Table 5.1):

Variable	Association	Direction	Comments
Valley location	yes	n/a	Consistent across years
Shading intensity	yes	negative	Consistent across years
Habitat type	yes	n/a	Consistent across years, occurrence and patch number only
Sediment patch size	minimal	positive	Inconsistent
Sediment patch number	nil	nil	No evidence of association
Vegetation height	yes	negative	Inconsistent across years, patch no & abundance
Vegetation type	yes	n/a	Inconsistent across years, strong association with *Hordeum vulgare*. Overall strongly associated with abundance & occurrence, weakly with occurrence and patch number
Substrate	nil	nil	No evidence of association
Evidence of herbivory	nil	nil	No evidence of herbivory found
River volume	nil	nil	No evidence of association

Table 5.1 Environmental variables (including evidence of grazing), and their association with *E. guttata* occurrence and abundance

5.1.1 Comparison to Truscott, et al. (2008a)

The key differences between this study and those of Truscott, et al. (2008a) are summarised in Chapter 2, figure 2.10. While the methodology of this study and that of Truscott, et al. (2008a) differed somewhat in terms of approach (such as use of Ellenberg indicators), key variables such as shading, mean vegetation height and vegetation type agreed, with some reservations: I considered using the number of trees and canopy cover combined, as in Truscott, et al. (2008a), as a means of calculating total shade cover for this study, however due to equipment constraints the previously noted method was adopted instead and the number of trees retained as a separate variable. The use of Ellenberg indicators in the Truscott, et al. (2008) paper roughly compares with the vegetation type category as used in this paper; the conclusion of a high light demand species, *Hordeum vulgare*, being associated with *E. guttata* presence agrees with the conclusions of Truscott, et al. (2008a). Again, this must be regarded with some caution if applying these finding s to individual species in New Zealand as it relies on a single species as evidence, rather than a group of species with similar characteristics as in the Ellenberg indicators.

The expected positive effect of river volume, sediment patch area and number on *E. guttata* was not observed, as was the effect (and indeed presence) of herbivory. I hypothesise that the lack of effect of river volume is in part due to differences in the studies; my study consisted of sections of primary waterway of 1-2km length, with relatively little gain in altitude. Truscott, et al. (2008a) studied an entire catchment, with its network of much smaller waterways. As such, inclusion of data from all the numerous smaller waterways found in a given catchment may reveal a hidden effect of river volume.

Objective 1) The survey results in general suggest that the findings of Truscott, et al. (2008a) may be applied with some caution to New Zealand habitats, at least within the Banks Peninsula region. The divergences in this survey from their findings are hypothesised to be the result of untested factors or limited granularity in the survey.

Objective 1a) Consistency across years was somewhat poor. This and the results of a PCA conducted on site variables suggests that significant environmental variables are yet to be considered in this model.

Objective 2) The results of the survey indicate that the populations of *E. guttata* may be invasive, however a closer study of individual patches is required to conclusively demonstrate this.

5.2 Testing for an overwintering seed bank

Seed banks play a major role in landscape-level persistence of weed species (Goodson, et al., 2001). *E. guttata* has previously been identified as forming a persistent seed bank (Goodson, et al., 2002; Elderd and Doak, 2006) however the magnitude of germinable seed content has been somewhat inconsistent, Truscott, et al. (2006) found a very small (6 seedlings from 20 soil cores) seed bank in their study in Aberdeenshire, Scotland. A glasshouse germination experiment (Chapter 3) was conducted to determine whether *E. guttata* forms a germinable, overwintering seed bank in the Banks Peninsula region. In this experiment, soil samples were

taken from three valley locations previously visited for the survey in Chapter 2. Samples were taken immediately prior to the spring growth period, when plants were still growing young shoots but had not flowered yet. To assess whether seeds became dormant over winter, a second set of samples was taken from these locations immediately after flowering ceased, but before the first frosts in autumn. Germination was monitored over a five-week period, and a total seedling count was taken at the end of this period.

If the first set of samples produce *E. guttata* seedlings, then the Banks Peninsula populations do produce a persistent, overwintering seed bank, as no other seed inputs since the last flowering season have been identified. If the second set produce seedlings, then the seed can be assumed to have a limited or absent dormancy period, not requiring cues such as vernalisation to initiate germination. However, if both sets show no seedlings, then the seed must have one or more of these traits; a) have such a low fertility rate as to preclude germination from a seed bank, b) have such low survivability that a seed bank does not persist or c) have a period of dormancy that is longer than the 6-month interval assessed.

Glasshouse experiments showed:

1) In the first set of samples, the three locations showed a mean seedling count of 0.68 (sd. 1.898) seedlings per litre of soil (20cmx20cmx2.5cm) for a total of 49 seedlings from 79 samples. This result is similar to that found by Truscott, et al. (2006) in Scotland.
2) In the second set, the three locations showed a mean seedling count of 14.78 per litre of soil (20cmx20cmx2.5cm) for a total of 887 seedlings from 60 samples.

A consistently higher mean germination rate (~2.3x) was found in samples across both sampling times from Orton-Bradley Park. This result strongly suggests that one or a combination of factors (heterogeneity of seed deposition, valley-level variance or local adaptation) may be at work. Of these, heterogeneity is most likely the cause, as distribution of both seeding plants and seed banks may be strongly influenced by environment (Truscott, et al., 2006; Warr, et al., 1993). Kaituna Valley and Te Oka were also notable, as Kaituna valley was expected to have a much greater *E. guttata* seedling count that was observed, and in fact Te Oka had the higher rate of the two.

5.3 Relative impact of shade and competition on *E. guttata* performance metrics

The objective of Chapter 3 was to examine the performance of clonal plants from a single parent growth in Orton-Bradley Park subjected to two kinds of stress; shade and interspecific competition, compared to controls. Experiments that study performance under selected environmental stressors have potential to improve understanding of selective pressures, physiological trends and trade-offs in function and form that may not be evident under normal conditions (Pigliucci, 2005).

For the two stressors, (shading intensity and competition), combined in 6 varying treatments over two experiments, only the shading intensity treatment showed a significant effect on performance measures. Overall, no effect of competition was observed. This result suggests that the trend observed in Chapter 2 of *E. guttata* presence being associated with *Hordeum*

vulgare is likely the result of common ecological niche traits responding to local environmental conditions and not the result of an interactive relationship, facilitative or otherwise.

5.4 Summary and future work

5.4.1 Summary

Six distinct valley locations, representing different habitat types and trends in land usage were surveyed in Banks Peninsula. 221, 50m sections sites were surveyed across the six valley locations, three of which were resurveyed the following year. Analysis of local environmental variables found the key factors limiting the spread of *Erythranthe guttata* were, in order of precedence; Shading intensity, characteristics of local vegetation (type and height) and habitat type. This contrasts with the work of Truscott, et al. (2008a), who conducted a similar survey in rural Scotland. From this work, *E. guttata* abundance and occurrence was expected to be strongly associated with sediment patches. No such significant association was found in this study, however further work is required to fully resolve this and other differences.

Concurrently with the field survey, a further two experiments were conducted; An experiment looking for evidence of a persistent soil seed bank using soil samples from the three valleys with populations of *E. guttata*, and a shading/competition greenhouse experiment. The seed bank experiment found evidence of a persistent soil seed bank, however whether this is persistent across multiple years or relies on constant seed inputs in unclear. Seed germination between valleys was quite inconsistent, in particular Orton-Bradley Park showed a significantly higher rate of seed germination than the other two valleys.

The shading experiment found that competition had no significant effect on plant performance metrics either alone or in combination with varying levels of shading intensity. It is most likely therefore that the observed association between *E. guttata* occurrence and *Hordeum vulgare* presence as a neighbour species is due to a shared ecological niche.

5.5 Future work

There is a considerable gap in the academic literature for a comprehensive study of the ecology of *E. guttata* in New Zealand, particularly around reproductive strategy, soil seed banks and factors affecting distribution in other habitats. Two particularly interesting avenues of research are highlighted by this thesis. (1) A survey similar to that in Chapter 2, but on a more granular scale to capture even more detailed data on factors affecting occurrence and abundance. In particular, the inclusion of soil chemistry data has potential to explain trends in plant species dispersal (Burke, et al., 1998). (2) A study into the overwinter survival rate of seed in New Zealand soils; how the relative seed fertility rates, pollination dynamics and other aspects of sexual reproduction influence total seedling population between a range of different habitat types. Of interest is comparing the results of the above areas of study between the North and South islands of New Zealand, due to the broad variation in climatic conditions between these areas. A particular location of interest to study in Banks Peninsula is Orton-Bradley park, due to the considerably higher (~2.3x) rate of seed germination found in the area.

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Appendix 1

Permanent photo points established during survey experiment.

Camera used: Canon EOS M5

Name	Latitude	Longitude	Description
HIN 1	-43.80989418	173.0318865	Hinewai access path. 5m down path past sign denoting *Hoheria angustifolia*. Facing uphill along the path
KAI 1	-43.74407808	172.6865514	Top of large flat rock overlooking River bank. Facing due west.
KAI 2	-43.74344149	172.6869903	Outside, downstream bank of river elbow facing upstream
OB 1	-43.65914982	172.7078341	Northern edge of river ford. West bank of river. Facing due SE

OB 2	-43.66003206	172.7077789	Top of large rock, southern edge of river bend. Facing due north
OB 3	-43.66193889	172.7087132	West bank of river. On the sign of Hunters Gully. Facing due north
TOK 1	-43.84990899	172.772647	15m upstream of bridge. Western bank facing east. Camera 1.4m elevation
TOK 2	-43.84894768	172.7736442	3m west of small ford.
TOK 3	-43.84894917	172.7738843	4m due south, 10m due east of ford. Adjacent to fence strainer

Appendix 2

Habitat classifications used in Chapter 2

Category	Abbreviation	Description
Bush	Bush	Primary/secondary native growth, consisting generally of native species. Includes large native trees, shrubs and dense undergrowth
Developed Grassland	DG	Monocultural growth. Generally *Lolium* spp. or *Hordeum vulgare*. Under cultivation, or otherwise consistently developed for human usage.
Undeveloped Grassland	UDG	Natural community with diverse species. Includes tussocks, native grasses, rushes/segdes/reeds etc. Has little human development (waterways, irrigation equipment, fences).
Forest	F	Mix of exotic and native trees, generally with less undergrowth and shrubs than Bush habitat. Most often a planted stand, rather than natural regrowth.

Appendix 3

Vegetation type classifications used in Chapter 2

Category	Species/genera included	Habitat associated
Fern	Members of *Polypodiales,* particularly genus *Blechnum*, *Cyathea* and *Asplenium*	Bush
Barley	*Hordeum vulgare*	Developed and Undeveloped Grassland
Mixed Tussock and Grasses	Heterogenous tussocks and grasses, includes *Poa cita*, *Briza* spp. and *Festuca* spp. as well as *Hordeum vulgare* and	Developed and Undeveloped Grassland

	Lolium spp. Also includes areas with stands of *Austroderia*	
Rubus spp.	Various spp. most commonly ruderal *Rubus fruticosus* L.	Forest and Undeveloped Grassland
Thistle/Nettles	Includes *Cirsium vulgare, Cirsium arvense, Urtica urens* and *Urtica ferox*	Bush, Forest, Developed and Undeveloped Grassland
Tussock	Includes *Poa cita, Briza* and *Festuca* spp.	Undeveloped Grassland
Flax	*Phormium* spp. (generally *P. tenax*)	Developed and Undeveloped Grassland
Other	Unidentified species including some exotics (ie. *Digitalis* spp., various *Coprosma* spp.). Includes rushes, reeds and sedges (*Poaceae, Juncaceae and Cyperaceae* respectively)	Bush, Forest and Developed Grassland

Appendix 4

Valley location environmental characteristics

Row Labels	**HIN**	**KAI**	**MTV**	**OB**	**SUM**	**TOK**
Average river depth (cm)	49	62	8	35	1	24
Average river width (cm)	373	452	75	310	64	129
Average of No. trees	59	6	7	32	8	25
Total sediment patches	5	4	23	13	1	4
Average sediment patch size (cm2)	397	613	1009	1379	313	160
Average vegetation height (cm)	29	45	63	38	71	29
Average shade %	76%	7%	7%	61%	24%	50%

Total sections surveyed	34	23	43	38	48	35
Most common substrate (count in brackets)	R (32)	R (16)	C/RC (21/17)	R (33)	RC/R (15/24)	R (34)
Most common habitat (count in brackets)	Bush (34)	DG 17)	UDG (31)	Forest (25)	UDG (33)	Bush (25)
Most common vegetation type (count in brackets)	Fern (33)	Barley (18)	Mixed Tussock and Grasses (35)	Barley/Fern (16/19)	Mixed Tussock and Grasses (19)	Barley/Fern (23/11)